MONTPELLIER SUPAGRO
Centre International d'Études Supérieures en Sciences Agronomiques

THESE

pour obtenir le grade de

DOCTEUR DE MONTPELLIER SUPAGRO

Discipline : Biologie de l'évolution et écologie

École Doctorale : Systèmes Intégrés en Biologie, Agronomie, Géosciences, Hydrosciences et Environnement

Présentée et soutenue publiquement

par

Sébastien VILLÉGER

le 8 décembre 2008

Dynamique de la diversité fonctionnelle des communautés de poissons (Lagune de Terminos, Mexique)

JURY

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M^{me} Julia RAMOS MIRANDA, Professeur, Université de Campeche	Co-directrice de thèse
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Résumé

Un des enjeux majeurs de l'écologie est de comprendre comment les changements globaux affectent la biodiversité et quelles en sont les conséquences sur le fonctionnement des écosystèmes. Dans cette perspective, la diversité fonctionnelle des communautés est un outil clé permettant de lier l'environnement, la structure des communautés et les propriétés écosystémiques. L'objectif de cette thèse est donc d'améliorer la compréhension de la dynamique de la diversité fonctionnelle (i) face à des conditions environnementales naturellement variables et (ii) face à des perturbations d'origine anthropique.

Dans un premier temps nous avons mis en place un socle méthodologie nous permettant de (1) définir la niche fonctionnelle des poissons à partir de traits fonctionnels et (2) de quantifier les diversités fonctionnelles intra (α) et inter (β) échantillons avec de nouveaux indices. Dans un second temps nous avons étudié la dynamique spatio-temporelle de la structure fonctionnelle des communautés ichtyologiques et nectoniques peuplant la lagune de Terminos (Mexique). Cet écosystème estuarien tropical est un modèle d'étude adapté à notre problématique car il présente une forte variabilité environnementale, une forte diversité biologique et est sous forte pression anthropique.

Nous avons mis en évidence une stabilité de la structure fonctionnelle et trophique des communautés face aux gradients environnementaux très marqués, et donc malgré un fort taux de remplacement des espèces entre les communautés. Cette stabilité est due à la dominance de quelques groupes fonctionnels à l'intérieur desquels les espèces se remplacent suivant leurs preferendums environnementaux. Néanmoins, à plus long terme, nous avons démontré qu'une portion de la lagune avait subi une perte de diversité fonctionnelle et ce malgré une augmentation de la richesse spécifique. Ce paradoxe est à relier au remplacement des espèces inféodées aux herbiers de phanérogames par des espèces plus estuariennes.

Mots clés : traits fonctionnels, indices de diversité fonctionnelle, écosystème estuarien, gradient environnemental, changements globaux, téléostéens, necton, Golfe du Mexique

Abstract

One of the main challenges in ecology is to understand how global changes affect biodiversity and what are the consequences on ecosystem functioning. In this perspective, the functional diversity of communities is a cornerstone since it allows linking environment, community structure and ecosystem properties. The aim of this thesis is thus to improve the understanding of functional diversity dynamic (i) in relation to natural variability of environmental conditions and (ii) under anthropogenic disturbances.

As a first step we have developed a new methodological framework allowing to (1) describe fish functional niches based on functional traits, and (2) to quantify functional diversity within (α) and among (β) sites thanks to new indices. In a second step we have studied the spatio-temporal dynamic of the functional structure of fish and nektonic communities from the Terminos lagoon (Mexico). This tropical estuarine ecosystem is an appropriate ecological model for our problematic as it is characterized by a strong environmental variability, a high biological diversity and is under a strong human pressure.

We have put in light the stability of the functional and trophic structures of communities along environmental gradients, despite a very strong species turnover. This stability is determined by the dominance of a couple of functional groups inside which species are replacing each others according to their environmental preferences. However, at a long-term scale, we have demonstrated a functional diversity loss in a part of the lagoon despite an increase of species richness. This paradox has to be related to the decrease of species associated to seagrass and the increase of more estuarine species.

Key-words: functional traits, functional diversity indices, estuarine ecosystem, environmental gradient, global changes, teleostian, nekton, Gulf of Mexico

La science est un jeu dont la règle du jeu consiste à trouver quelle est la règle du jeu

François Cavanna

Remerciements

> Le commencement de toutes les sciences,
> c’est l’étonnement de ce que les choses sont ce qu’elles sont.
>
> *Aristote*

Écrire des remerciements n’est pas une chose facile et j’espère que les lignes qui suivent résument toute la gratitude que j’éprouve pour les personnes citées.

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Chapitre 1.

Les changements globaux, la biodiversité et le fonctionnement des écosystèmes

The fate of biological diversity for the next 10 million years will almost certainly be determined during the next 50–100 years by the activities of a single species. That species, Homo sapiens, is ≈200,000 years old. It has been fabulously successful by ecological standards: it boasts as-yet-unchecked population growth and a cosmopolitan distribution, and it has vanquished its predators, competitors, and some of its parasites. The fossil record suggests that the typical mammal species persists for approximately one million years, which puts Homo sapiens in mid-adolescence. This is a fitting coincidence, because Homo sapiens is now behaving in ways reminiscent of a spoiled teenager. Narcissistic and presupposing our own immortality, we mistreat the ecosystems that produced us and support us, mindless of the consequences.

Ehrlich & Pringle 2008

1.1 Un monde sous pression anthropique croissante

Homo sapiens est une espèce relativement récente puisqu'elle n'est apparue qu'il y a 200 000 ans. Néanmoins, si son accroissement a été lent durant la plus grande partie de son existence, il s'est considérablement accéléré depuis 200 ans. En effet, en l'an mille, la Terre ne comptait que 300 millions d'êtres humains, puis 1 milliard en 1800, 2 milliards dans les années 1920 et 6 milliards en 1999. Cette augmentation exponentielle est supposée se stabiliser en 2050 autour de 9 milliards d'habitants (ONU 1999). La population humaine aura alors été multipliée par neuf en deux siècles et demi.

Cette croissance de la population s'est aussi accompagnée d'un fort développement économique et technologique. Ce dernier est notamment caractérisé par l'utilisation massive de combustibles fossiles (charbon, pétrole, gaz) pour produire de l'énergie. Plus généralement, les populations humaines utilisent de plus en plus les ressources à disposition. Par exemple, la demande en eau douce pour l'agriculture, l'industrie et la consommation domestique a plus que doublé depuis 1960 (WWF 2006) et plus de la moitié des stocks d'eau douce sont actuellement exploités (Postel *et al.* 1996). Par conséquent, l'empreinte écologique, mesurée comme la surface terrestre nécessaire pour assurer la totalité des besoins humains, a plus que triplé en 40 ans (WWF 2006). L'Homme a une telle influence sur l'environnement que certains auteurs qualifient la période récente d'anthropocène (Crutzen 2002).

1.2 Les changements globaux

Les impacts humains sont multi factoriels, interagissent entre eux et affectent tous les compartiments abiotiques et biotiques de notre planète (Figure 1.1). Ils sont regroupés sous le terme de changements globaux.

1.2.1 Le climat

L'aspect le plus médiatisé de l'influence humaine est certainement le réchauffement climatique. Il est engendré par un accroissement de l'effet de serre qui résulte principalement de l'augmentation de la concentration atmosphérique en dioxyde de carbone (CO_2) et en méthane (Hansen & Sato 2001). Cette augmentation est majoritairement due à la combustion massive de pétrole, de charbon et de gaz pour la production d'énergie (industrie, transports, chauffage). Depuis la révolution industrielle, la concentration en CO_2 a ainsi augmenté de plus de 30% (IPCC 2001). Le méthane est produit en moindre quantité mais sa concentration a augmenté de plus de 150% (IPCC 2001) et il engendre un effet de serre 20 fois plus fort que le CO_2 (Fuglestvedt *et al.* 2003).

La température moyenne à la surface de la Terre s'est en moyenne accrue de 0.6°C au cours du siècle passé (IPCC 2001) et la responsabilité des activités humaines dans cette augmentation ne fait plus débat dans la communauté scientifique (Oreskes 2004). Ce réchauffement affecte notamment le niveau des mers via la dilatation des océans et la fonte des glaciers (augmentation annuelle d'environ 1mm). Il modifie également le régime des précipitations et augmente la vulnérabilité de certaines régions aux épisodes extrêmes (sécheresses, canicules, cyclones).

Les changements climatiques affectent profondément les aires de répartition des espèces (Thuiller *et al.* 2005). Pour certaines espèces, le réchauffement climatique est même une cause d'extinction puisqu'il entraîne la disparition des conditions nécessaires à leur survie (Thomas *et al.* 2004). Le réchauffement climatique perturbe aussi la phénologie des organismes (Bradley *et al.* 1999). Cependant, les organismes ne répondent pas tous de la même manière au réchauffement. Cela peut engendrer des décalages entre les niveaux trophiques et donc provoquer une forte diminution des prédateurs lorsque la dynamique des proies n'est plus en phase (Stenseth & Mysterud 2002) ; par exemple entre les pics de ressources (ex : chenilles) et le pic des besoins énergétiques d'un prédateur (ex : la mésange bleue).

Outre ces effets progressifs à grande échelle, les extrema thermiques peuvent provoquer de profondes perturbations. Ainsi, en 1998 l'effet d'El Niño sur le Pacifique Ouest s'est traduit par un réchauffement des eaux de surface de plus de 1°C (Hoegh-Gudberg 1999). Ces températures anormales ont provoqué un stress chez les coraux qui s'est traduit par un blanchiment massif (du fait de l'expulsion des zooxanthelles symbiotiques colorées). 87% des récifs littoraux sur la Grande Barrière de Corail (Australie) ont été touchés par ce stress (Berkelsman & Oliver 1999). Or le blanchiment provoque des taux de mortalité pouvant atteindre 90% (Hoegh-Gudberg 1999). L'augmentation de la fréquence et de l'intensité de ces évènements extrêmes est donc une menace majeure pour les écosystèmes coralliens (Bellwood *et al.* 2004).

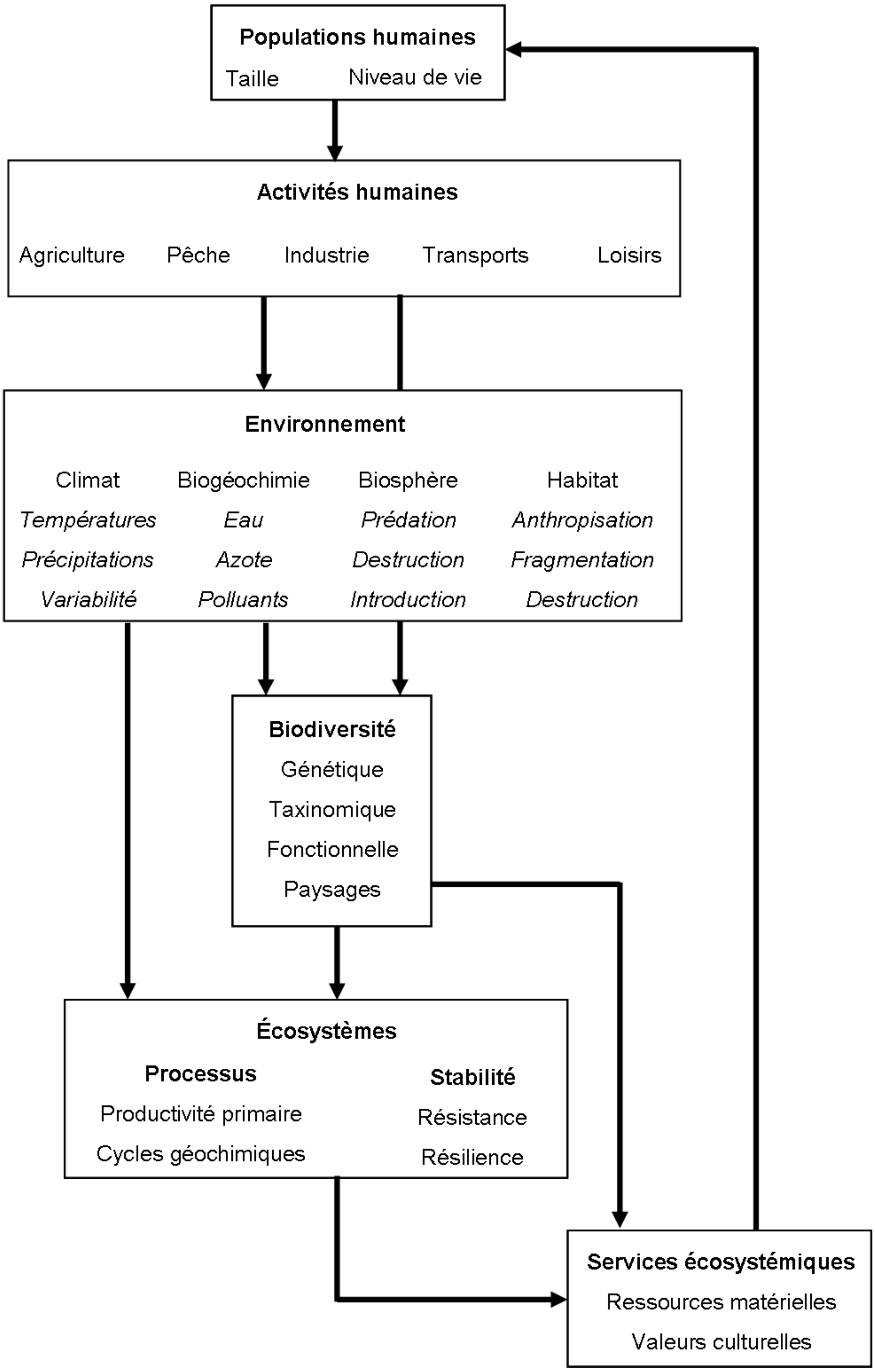

Figure 1.1. Schéma synthétique des causes et conséquences des composantes des changements globaux (adapté de Vitousek *et al.* 1997).

Les épisodes extrêmes peuvent aussi déclencher des changements biologiques ponctuels. Ainsi, la floraison des Posidonies en Méditerranée est extrêmement rare et semble induite par des températures inhabituellement élevées (Diaz-Almela *et al.* 2007).

L'effet à long terme des changements climatiques reste néanmoins difficile à prédire pour des écosystèmes complexes. Par exemple, pour les écosystèmes côtiers, le réchauffement climatique s'accompagne aussi de changements chimiques (acidification), de la modification de la distribution horizontale et verticale des organismes, de la disparition de certaines espèces clés et de l'introduction de nouvelles espèces (Harley *et al.* 2006). Ces effets sont parfois non linéaires et agissent en interaction voire même en synergie. Il est donc difficile de prédire leurs conséquences et de nombreux travaux sont encore nécessaires pour les évaluer.

1.2.2 Les flux géochimiques

Comme illustré précédemment à propos du carbone, tous les flux géochimiques sont aussi fortement modifiés par les activités humaines. L'exemple le plus frappant concerne le cycle de l'azote. En effet, la fixation industrielle, à partir de pétrole, de l'azote atmosphérique (N_2) excède aujourd'hui la fixation naturelle d'azote assurée par les microorganismes (Vitousek *et al.* 1997). Ainsi, l'utilisation d'engrais azotés chimiques en agriculture a été multipliée par huit depuis les années 1960 (Tilman *et al.* 2001). De même l'utilisation de pesticides a été multipliée par 6 entre 1955 et 1985 (Tilman *et al.* 2001). Ces pesticides et plus largement les polluants issus de l'agriculture et de l'industrie (notamment les métaux lourds) se retrouvent dans de nombreux organismes et engendrent des maladies (cf la maladie de Minimata due au mercure, Ninomiya *et al.* 1996) ou des troubles du développement (cf les perturbations hormonales dues à certains pesticides chez les amphibiens, Hayes *et al.* 2002).

L'introduction massive par l'Homme de composés azotés et phosphorés provoque de profonds bouleversements biotiques dans les écosystèmes. Ceci est particulièrement visible pour les écosystèmes aquatiques côtiers et lacustres qui subissent le phénomène d'eutrophisation (Cloern 2001, IFREMER 2001). En effet, dans les conditions naturelles, l'azote et le phosphore sont des ressources limitantes pour la production primaire. Lorsqu'elles deviennent abondantes, elles permettent donc une augmentation considérable de la production primaire. En réalité ce sont certains organismes adaptés à ces fortes concentrations qui sont favorisés, particulièrement les macroalgues ou le phytoplancton suivant les conditions hydrologiques. Cette augmentation de la productivité primaire n'est pas totalement absorbée par les consommateurs secondaires et entre donc en décomposition

(Baird *et al.* 2004). Ces processus consomment une grande partie de l'oxygène dissous et l'écosystème devient hypoxique, ce qui entraine la disparition des nombreuses espèces ne pouvant survivre dans de telles conditions (Gray *et al.* 2002). Ainsi, les zones côtières en hypoxie sont de plus en plus nombreuses et étendues à la surface du globe (Diaz 2001, Diaz & Rosenberg 2008).

Il est à noter que la végétation aquatique joue un double rôle dans ce processus (McGlathery *et al.* 2007). En effet, les herbiers de phanérogames préviennent l'eutrophisation en stockant la matière organique dans leurs tissus et dans le sédiment. Cependant lorsque la concentration en nutriments augmente, ils sont progressivement remplacés par les algues, meilleures compétitrices (McClelland & Valiela 1998, Orth *et al.* 2006). Les algues favorisent alors l'eutrophisation de par leur court cycle de vie, leur faible rétention de matière organique et leur mobilité (McGlathery *et al.* 2007). Cet exemple illustre par ailleurs le concept de changement de phase, qui désigne une perturbation majeure de la structure d'un écosystème engendrant une modification durable de son état d'équilibre (Folke *et al.* 2004).

1.2.3 La prédation et les introductions

Homo sapiens était jusqu'à il y a 10 000 ans chasseur-cueilleur. En d'autres termes, comme tous les animaux, l'Homme se nourrissait en chassant et collectant des espèces sauvages. Malgré les faibles densités de populations d'alors, la prédation humaine est pourtant fortement suspectée d'avoir largement contribué à l'extinction des grands mammifères australiens et nord-américains il y a plus de 40 000 ans (Barnosky *et al.* 2004). Malgré le développement croissant de l'agriculture, l'impact des prélèvements dans les populations naturelles est demeuré conséquent au cours des siècles suivants. Plus récemment, l'augmentation exponentielle de la population humaine et les développements technologiques n'ont fait que décupler l'impact direct de l'Homme sur les autres espèces.

Ainsi, dans l'Atlantique Nord la population des baleines à bosse est passée de 240 000 individus à seulement 10 000 aujourd'hui sous l'effet de la chasse baleinière intensive durant le 19ème siècle (Roman & Palumbi 2003). La population de dugongs au sud de la Grande Barrière de Corail (Australie) a subi une diminution d'un facteur 75 passant de plus d'un million d'individus il y a 2000 ans à moins de 15 000 aujourd'hui sous l'effet des chasseurs aborigènes et des premiers colons (Jackson *et al.* 2001).

Le tonnage de poissons débarqués a quant à lui augmenté de plus de 50% entre 1970 et 1990 (MEA 2005). Il faut souligner que ces chiffres ne tiennent pas compte des prises annexes, souvent rejetées mortes à la mer (Stevens *et al.* 2000). 60% des pêcheries sont désormais surexploitées ou fermées (Vitousek *et al.* 1997). Par ailleurs, les pêcheries ciblent des espèces de plus en basses dans la chaine trophique, au fur et à mesure que les stocks s'épuisent (Pauly *et al.* 1998). Les top-prédateurs ont ainsi vu leurs populations décliner dramatiquement (Myers & Worm 2003). Certaines espèces de requins du Golfe du Mexique ont été quasiment exterminées par la surpêche (Baun & Myers 2004). Or la disparition de ces prédateurs n'est pas sans conséquence pour les autres espèces. Par exemple, sur la côte Atlantique des États-Unis, la diminution des effectifs de grands requins a provoqué une augmentation des populations de leurs proies (raies) et par effet de cascade une diminution des proies de ces dernières (pétoncle), qui en l'occurrence étaient aussi ciblées par la pêche (Myers *et al.* 2007).

L'Homme présente également la caractéristique de tuer des êtres vivants pour d'autres raisons que l'approvisionnement alimentaire. Les forêts sont largement exploitées et le bois sert principalement au chauffage, à la construction et à l'industrie papetière. Certains végétaux sont aussi supprimés des surfaces agricoles pour éviter la compétition avec les espèces d'intérêt agronomique. De même, les animaux (insectes, rongeurs) potentiellement ravageurs de cultures sont massivement détruits par les pesticides. Enfin, l'Homme a aussi largement exterminé les autres prédateurs apicaux, en partie parce qu'ils représentaient un danger direct mais surtout parce qu'ils sont une menace pour les troupeaux (Breintenmoser 1998). Ainsi, les populations de loups et d'ours ont été décimées à plus de 95% en Europe et en Amérique du Nord (Berger *et al.* 2001).

Par ailleurs, les flux de populations humaines et de biens, qui n'ont cessé de s'intensifier, ont engendré des introductions d'espèces « exotiques » dans des écosystèmes qu'elles n'auraient pas pu atteindre naturellement (Levine & D'Antonio 2003, Sax & Gaines 2003). Ces introductions d'espèces exotiques engendrent des perturbations majeures (Mack *et al.* 2000), notamment via la prédation des espèces natives ou la préemption des ressources (par exemple via le broutage). Par exemple, l'introduction de la truite (*Salmo trutta*) en Nouvelle-Zélande a provoqué la disparition d'espèces de poissons endémiques, a modifié la distribution des invertébrés herbivores et par cascade a favorisé la croissance des algues. Au final, cette espèce invasive prédatrice exerce un contrôle sur tous les flux de nutriments et perturbe ainsi la structure des écosystèmes où elle a été introduite (Townsend 2003).

1.2.4 Les habitats

L’Homme a aussi largement modifié les habitats naturels. La surface des terres occupées par l’agriculture représente désormais plus du quart de la surface terrestre (Vitousek *et al.* 1997). La production végétale et l’élevage nécessitent en effet de larges surfaces de terres arables ou de prairies. Ces surfaces ont souvent été gagnées sur la forêt depuis plusieurs milliers d’années (Carcaillet 1998) mais actuellement ce sont les forêts tropicales qui sont les plus touchées (Nepstad *et al.* 1999, Achard *et al.* 2002). Certains aménagements tels les barrages bouleversent aussi considérablement les écosystèmes en perturbant leur connectivité (Nilsson *et al.* 2005). Plus localement, l’urbanisation et les voies de communication modifient aussi les paysages. Les habitats sont donc affectés dans leur étendue, leur répartition et leur connectivité. Ceci a des impacts majeurs sur les communautés biologiques et le fonctionnement des écosystèmes (Fahrig 2003).

Ainsi, dans les écosystèmes côtiers tropicaux, la connectivité entre les différents types d’habitats joue un rôle positif sur la diversité et l’abondance des poissons (Layman *et al.* 2004). Par conséquent la destruction de la mangrove ou d’herbiers de phanérogames va perturber non seulement les communautés associées mais aussi les communautés vivant sur les récifs coralliens (Dorenbosch *et al.* 2005, 2007).

1.3 Une perte de biodiversité sans précédent depuis 65 millions d’années

La Terre a subi de nombreuses perturbations depuis sa formation il y a 4,5 milliards d’années. Plus particulièrement, depuis l’apparition de la vie, cinq grandes crises d’extinction ont pu être mises en évidence dans les enregistrements fossiles (Hallam & Wignall 1999). La crise Permo-triasique, datée d’environ 250 millions d’années, fut la plus massive avec des taux d’extinction de 90% (Stanley & Yang 1994, Benton & Twitchett 2003). La crise la plus récente est la crise Crétacé-Tertiaire. Elle est caractérisée par la disparition des dinosaures et de bon nombre d’autres espèces, et a permis la radiation des plantes à fleurs, des insectes et des mammifères (Labandeira & Sepkoski 1993, Springer *et al.* 2003). Ces crises d’extinction sont en fait définies par des taux d’extinction bien plus élevés que la moyenne. D’après les enregistrements fossiles, il est possible d’estimer qu’en moyenne moins d’une espèce sur mille disparaît par millénaire (pour les organismes marins, MEA 2005). Or, le taux d’extinction observé actuellement est presque 100 fois plus fort. Ainsi, parmi les 26 220 espèces prises en compte par l'UICN (Baillie *et al.* 2004), 733 sont éteintes et 7266 en danger d'extinction. Or cette étude ne considère qu'une petite portion des 1,5 millions d'espèces décrites puisqu'il reste probablement plus de 7 millions d'espèces à décrire. Pour les poissons, sur les 1700 espèces recensées presque la moitié (46%) sont menacées (Baillie *et al.* 2004). Cette proportion monte à plus de 80% pour les crustacés (Baillie *et al.* 2004).

Cette pression massive sur les êtres vivants est à relier aux changements globaux dont les différentes composantes agissent simultanément et parfois même en synergie sur les écosystèmes (Sala *et al.* 2000). Par exemple, une espèce de poisson qui est surpêchée voit ses stocks diminuer rapidement. Si en plus, certains de ses habitats clés sont pollués ou détruits (par exemple ses frayères), ou si des espèces introduites entrent en compétition avec elle ou la consomment, alors cette population subira un faisceau de facteurs négatifs. Elle sera par conséquent encore plus vulnérable au facteur pêche (Reynolds *et al.* 2005).

Plus généralement, la diversité des êtres vivants, de leurs assemblages, et même des paysages est menacée à l'échelle du globe. Après l'adoption de la Convention sur la Diversité Biologique en 1992, la notion de biodiversité et la nécessité de la préserver s'est largement répandue auprès du grand public. Néanmoins, la biodiversité est souvent confondue avec la notion de richesse spécifique. En réalité elle est définie comme le nombre, l'abondance, la composition, la distribution spatiale et les interactions des génotypes, populations, espèces, traits fonctionnels et paysages dans un système donné (tiré de Diaz *et al.* 2007). C'est donc un concept multi-facettes à la fois en terme d'échelle d'étude (du gène à l'écosystème) et de variable mesurée (richesse, régularité, disparité, connections).

Par conséquent, s'il est clair que le nombre d'espèces est en rapide déclin, il est crucial d'aller plus loin que ce simple estimateur et d'étudier toutes les tendances actuelles des différentes facettes de la biodiversité (Purvis & Hector 200). Ceci afin d'offrir un « panorama » global sur l'état de la diversité biologique au sens large. Par exemple, une espèce peut voir sa population rester stable tout en présentant une forte perte de diversité génétique. Par ailleurs, il faut aussi prendre en compte l'identité et la biologie des espèces qui disparaissent. En effet, l'impact de la perte d'une espèce sur la biodiversité est très différent selon qu'il subsiste ou non une espèce biologiquement très proche dans l'écosystème. Cet exemple souligne l'importance de la conservation de l'originalité biologique (Mouillot *et al.* 2008). De même, certaines espèces dites espèces-clés, ingénieurs ou fondations sont plus importantes que d'autres pour le fonctionnement et la structuration des écosystèmes (Ellison *et al.* 2005). Par exemple les palétuviers formant les mangroves stabilisent la structure physique de la côte, préviennent l'eutrophisation des récifs coralliens et des herbiers adjacents et servent de nurserie à bon nombre d'espèces.

1.4 Fonctionnement et services des écosystèmes

La prise de conscience globale concernant les menaces que les changements globaux induits par l'Homme font peser sur les autres êtres vivants (Chapin *et al.* 1997), a accéléré les programmes de recensement et de conservation des espèces. Ces mesures de conservation n'impliquent souvent que le niveau spécifique. Les exemples les plus visibles concernent les écosystèmes riches en espèces (« hotspot », Myers *et al.* 2000) ou des espèces patrimoniales telles que l'éléphant d'Afrique ou l'ours brun d'Europe. Néanmoins, si les êtres vivants ont une valeur intrinsèque liée tout simplement à leur existence, ils assurent aussi un certain nombre de processus écologiques au sein des écosystèmes. Il est donc primordial de définir ces propriétés écosystèmiques et de comprendre comment les organismes vivants les affectent.

1.4.1 Le fonctionnement des écosystèmes

Tous les êtres vivants ont besoin d'énergie et de matière pour assurer leur croissance, leur survie et leur reproduction. Ils sont par conséquent les acteurs d'une grande variété de flux (Begon *et al.* 2006).

Pour les organismes autotrophes, ces flux concernent principalement le carbone, l'azote, le phosphore et l'eau (pour les espèces non aquatiques). Tous ces éléments sont à la base de la production primaire qui va elle même être utilisée par les organismes hétérotrophes pour la production secondaire. Les flux de matière s'effectuent donc à l'intérieur des organismes mais aussi entre eux le long de la chaîne trophique, et même à travers l'espace et le temps via les migrations et le stockage de matière. Tous ces flux de matière et d'énergie sont regroupés sous le terme de processus écosystémiques (Figure 1.1).

Les êtres vivants influencent directement ces processus en les assurant mais aussi indirectement en affectant les flux naturels. Par exemple, les herbiers de phanérogames utilisent les nutriments du sédiment pour leur croissance mais d'un autre côté favorisent l'accumulation des sédiments par leur structure physique (Orth *et al.* 2006).

1.4.2 La stabilité des écosystèmes

Outre le fonctionnement, les êtres vivants influencent aussi la stabilité des écosystèmes vis-à-vis des perturbations. Une perturbation est définie comme un évènement détruisant tout ou partie de la biomasse. Les exemples les plus fréquents sont les feux, les cyclones ou les crises hypoxiques pour les écosystèmes aquatiques (Diaz 2001).

La stabilité peut être décomposée en deux facettes : la résistance et la résilience. La résistance correspond à la capacité d'un écosystème à limiter l'impact d'une perturbation. Par exemple, les mangroves offrent une protection vis-à-vis des vagues (Alongi 2002) en particulier lors des tsunamis (Danielsen *et al.* 2005). La résilience correspond à la capacité du système à revenir à son état initial. Hughes *et al.* (2007) ont ainsi mis en évidence le rôle primordial des poissons herbivores dans la résilience des écosystèmes coralliens après un épisode de blanchiment. En effet, durant la phase de recolonisation, les pousses de corail sont en compétition avec les algues qui se développent sur le squelette calcaire des coraux morts. Les poissons herbivores, en contrôlant la densité et la taille de ces algues, favorisent donc la repousse des coraux, moins bons compétiteurs. A l'inverse, en leur absence, le système change de phase et devient irrémédiablement dominé par les macroalgues. De manière encore plus intéressante, il a été démontré que la diversité des herbivores influence significativement leur action (Bellwood et al. 2006a). En effet, la notion globale d'herbivores regroupe en réalité une grande diversité d'espèces ciblées. C'est donc la synergie entre espèces qui permet la résilience optimale.

1.4.3 Les services écosystémiques fournis aux populations humaines

Le fonctionnement et la stabilité des écosystèmes sont des concepts écologiques sans valeur intrinsèque. Plus concrètement, le fait que la productivité primaire dans les eaux très oligotrophes soit faible n'est pas un signe de mauvais fonctionnement de l'écosystème. Écologiquement parlant, les récifs coralliens, riches en espèces et en biomasse, ne sont pas « meilleurs » que les eaux pauvres du grand large.

Néanmoins, il est évident que les populations humaines profitent directement et indirectement du fonctionnement et de la stabilité des écosystèmes. Ces bénéfices sont désignés par le terme de services écosystémiques (Constanza *et al.* 1997). Ils sont en fait très variés et regroupent des bénéfices matériels et culturels. Certains sont issus directement des organismes vivants comme l'approvisionnement en nourriture (glucides, protéines, lipides, animaux ou végétaux), en matériaux (bois, cuir), en combustible (bois, charbon, pétrole) ou en « outils » (antibiotiques des *Penicilium,* GFP d'*Aequorea victoria*). D'autres découlent du fonctionnement des organismes au sein de l'écosystème, comme par exemple la formation des sols, la régulation du cycle de l'eau et des nutriments. Enfin, certains sont centrés sur des valeurs culturelles. Par exemple, les poissons de récifs coralliens sont au centre d'activités de loisirs, soit in situ à travers la plongée soit indirectement via l'aquariophilie. Le tourisme lié aux récifs coralliens (Australie, Floride et Caraïbes) représente une intense activité économique estimée à plus de 90 milliards de dollars par an à la fin des années 90 (Hoegh-Gudberg 1999). Par ailleurs, les récifs coralliens ont une haute valeur esthétique comme le montrent les nombreux films, photos ou jouets dont ils sont le sujet (Moberg & Foke 1999). Ils sont aussi l'objet de croyances religieuses dans de nombreuses populations.

Ces bénéfices spirituels se retrouvent aussi dans les zones urbanisées. Il a par exemple été démontré que les patients bénéficiant d'une vue sur un espace vert se rétablissaient mieux d'une opération chirurgicale que ceux ayant vue sur une zone aménagée (Ulrich 1984). Plus généralement, les espaces verts et la biodiversité urbaine offrent des bénéfices psychologiques aux populations citadines et ce d'autant plus fortement que la richesse biologique est élevée (Fuller *et al.* 2007).

Il est évident à travers ses exemples que la valeur de ces services écosystémiques est intimement liée au contexte économique et culturel. Le bois a beaucoup plus de valeur pour les populations ne disposant pas de combustibles fossiles ou d'électricité, ni d'autres matériaux de construction. Similairement, une même ressource peut voir sa valeur changer considérablement selon son utilisation. Ainsi un poisson récifal rapporte plus de devises via la plongée ou l'aquariophilie que s'il est consommé.

Par ailleurs, il est nécessaire de souligner que si certains services sont apparemment « gratuits », leur valeur n'en est pas moins importante. L'action des poissons herbivores qui entretiennent les récifs coralliens en empêchant les algues d'envahir les coraux n'a pas de valeur économique intrinsèque. Néanmoins, s'ils n'existaient pas, l'entretien artificiel du récif, si tant est qu'il soit techniquement réalisable, nécessiterait une quantité de main d'œuvre colossale. Ce coût global extrêmement élevé peut être vu comme la conversion en valeur marchande du « travail » effectué par les poissons herbivores des récifs.

Pour résumer, les êtres vivants assurent l'approvisionnement matériel des populations humaines et plus généralement contribuent à leurs bien être physique et mental.

1.5 Quelles sont les conséquences écosystémiques des changements de biodiversité?

Les services écosystémiques découlent du fonctionnement et de la stabilité des écosystèmes, eux mêmes largement influencés par les organismes qui les composent (Chapin *et al.* 2000). La conservation ne doit donc pas seulement suivre une philosophie de type « collection naturaliste » mais doit se fonder sur une démarche systémique. Quelles populations, espèces, et communautés devons nous préserver en priorité pour assurer la durabilité des processus écosystémiques ? Cette protection recoupe le principe du développement durable c'est-à-dire la transmission aux générations futures de ce dont nous avons nous mêmes hérité. Le préalable à cette question générale est d'étudier le lien entre la biodiversité et les propriétés écosystémiques.

1.5.1 L'effet de la richesse spécifique sur les processus écosystémiques

Durant plusieurs décennies, la biodiversité a été étudiée comme la variable résultante de contraintes environnementales et de contingences historiques et phylogénétiques (Whittaker 1965, Connell 1978, Gray 1981, Frontier 1985). Le début des années 90 marque alors un tournant avec la prise en compte de la biodiversité comme une variable prédictive du fonctionnement des écosystèmes (Mooney & Schulze 1993).

Les premiers travaux se sont focalisés sur la relation entre le nombre d'espèces et les propriétés écosystémiques (Tilman *et al.* 1994, Naeem *et al.* 1994, Hector *et al.* 1999). Ces études utilisant les communautés végétales comme modèle ont mis en évidence, par expérimentation, que le nombre d'espèces influençait positivement les processus écosystémiques telles que la productivité ou la résistance à l'invasion. Néanmoins, ces résultats ont été largement débattus, notamment sur le fait qu'il pouvait y avoir un effet confondant lié à l'identité des espèces (Huston *et al.* 1997, Grime 1998). En effet, plus il y a d'espèces dans un assemblage, plus il y a de chances qu'il y en ait une qui soit très performante pour le processus étudié ou résistante face aux perturbations. Ce « sampling effect » résulte d'un simple artefact statistique et n'a donc rien à voir avec une éventuelle complémentarité entre les espèces.

1.5.2 L'effet de la structure fonctionnelle des communautés sur les processus écosystémiques

L'utilisation de la richesse spécifique fait l'hypothèse implicite que toutes les espèces sont équivalentes. Or il est évident que les espèces diffèrent plus ou moins entre elles. Il est donc apparu nécessaire de considérer l'identité biologique des espèces. Les études suivantes se sont ainsi intéressées au nombre de groupes fonctionnels comme le « moteur » principal agissant sur les processus (Tilman *et al.* 1997, Hooper & Vitousek 1997). Ces groupes sont définis a priori à partir de caractéristiques biologiques communes, liées au métabolisme, à la taille ou à la reproduction (Lavorel *et al.* 1997).

D'autres études ont suggéré que les caractéristiques des espèces dominantes influençaient plus les propriétés écosystémiques que la richesse ou la composition en groupes fonctionnels (Wardle *et al.* 1997). Cette idée a notamment été développée par Grime (1998) sous le nom d'hypothèse du ratio de biomasse. Selon cette hypothèse, ce sont les quelques espèces dominantes et leurs caractéristiques qui déterminent les processus écosystémiques. Les espèces mineures influencent le fonctionnement à long terme en étant potentiellement de futures espèces dominantes si les conditions environnementales changent. Enfin, certaines autres espèces mineures ne sont en fait que transitoires, c'est-à-dire qu'elles ne persistent pas dans l'écosystème. Par conséquent, il est impératif de ne pas considérer seulement la composition d'une communauté mais de prendre aussi en compte sa structure en terme de distribution des abondances.

Cette approche de la diversité biologique par le biais des caractéristiques biologiques des espèces rejoint en fait le cadre méthodologique issu de l'écologie fonctionnelle. Cette dernière est une thématique très récente en écologie puisqu'elle s'est développée à la fin des années 80 (Calow 1987). A l'origine, elle était étroitement liée à l'approche évolutive par le biais de la notion de fitness (succès reproducteur). Ainsi, les traits fonctionnels sont définis comme des caractéristiques individuelles influençant la fitness via leurs effets sur la croissance, la survie et la reproduction (Calow 1987, Violle *et al.* 2007). Le principal avantage des traits fonctionnels est de proposer une caractérisation des communautés indépendamment de la taxinomie. Par exemple, il est plus intéressant de savoir que le brochet a un corps très allongé, un oeil relativement grand par rapport à sa tête et une nageoire caudale relativement haute par rapport à son pédoncule caudal, plutôt que de simplement connaître son nom latin *Esox lucius*. De manière moins provocante, il parait désormais évident que les relations interspécifiques et les liens entre l'environnement, la structure des communautés et le fonctionnement des écosystèmes sont principalement dictés par les traits fonctionnels des espèces et non par leur taxinomie (McGill *et al.* 2006).

1.5.3. Quels traits et quelles mesures de diversité fonctionnelle ?

Chez les végétaux, le choix de quelques traits pertinents a permis leur collecte pour un très grand nombre d'espèces et la mise en évidence de compromis évolutifs (Reich *et al.* 1997, Wright *et al.* 2004). Outre cette utilisation des données pour comparer les traits, il est surtout possible de comparer les différences entre espèces pour un ou plusieurs traits (Keddy 1992).

Compte tenu d'une part, du débat sur l'effet de la diversité sur les processus, et d'autre part de l'interrogation concernant les effets des changements environnementaux sur les espèces, les traits fonctionnels apparaissent donc comme un outil « clé » dans cette perspective (Suding *et al.* 2008). Lavorel & Garnier (2002) vont jusqu'à évoquer le Saint Graal qui consisterait en l'utilisation, d'une part de traits de réponse pour quantifier l'impact de l'environnement sur la composition des communautés, et d'autre part de traits d'effet pour quantifier l'influence des communautés sur les propriétés écosystémiques.

De nombreuses études ont ainsi analysé l'effet des contraintes environnementales sur les traits fonctionnels (McIntyre *et al.* 1995, Pakeman 2004, Garnier *et al.* 2007) et l'effet de certains traits sur les processus écosystémiques (Garnier *et al.* 2004, Kazakou *et al.* 2006). Néanmoins, la plupart de ces études ne considèrent qu'un seul trait et souvent en ne considérant que la valeur moyenne du trait pour la communauté. Afin d'aller plus loin dans l'étude du triplet environnement-diversité-fonctionnement des écosystèmes, il semble nécessaire de considérer la diversité fonctionnelle, et pour cela d'utiliser les abondances et les valeurs de traits de chaque espèce présente dans les communautés. De nombreux indices de diversité fonctionnelle ont été proposés depuis une dizaine d'années mais aucun ne fait consensus (Petchey & Gaston 2006). Par ailleurs, si l'effet de l'environnement sur la diversité fonctionnelle a été testé (Cornwell *et al.* 2006), il n'y a encore que peu d'études sur les effets des changements environnementaux sur la diversité fonctionnelle.

Des avancées dans la quantification de la diversité fonctionnelle devraient ainsi permettre d'améliorer la compréhension (1) de l'influence des contraintes environnementales sur la structure fonctionnelle des communautés et (2) de l'influence de cette structure fonctionnelle sur les processus écosystémiques.

1.6 Comprendre la structuration des communautés dans l’espace et dans le temps

Comme la structure fonctionnelle des communautés influence les processus écosystémiques, il est donc primordial de comprendre la structuration des communautés dans l’espace et dans le temps. Ce domaine de l’écologie, généralement désigné sous le terme d’écologie des communautés, s’intéresse donc aux relations entre les espèces et l’environnement mais également aux interactions entre les espèces elles mêmes.

1.6.1 La niche écologique

La notion de niche est ancienne et très largement employée en écologie. Toutefois, elle regroupe deux concepts bien distincts (Leibold 1995). Tout d’abord la niche telle que définie par Grinnell (1917) correspond à l’ensemble des conditions nécessaires à la survie d’une espèce, en terme d’habitat, de ressources et de prédation. Cette définition se rapproche de celle de Hutchinson (1957) qui formalisa ce concept à travers un espace multi dimensionnel où chaque axe correspond à une contrainte/ressource (Figure 1.2). Ce formalisme recoupe par ailleurs la pensée évolutionniste puisque la niche correspond aux conditions dans lesquelles une espèce peut assurer sa descendance et ainsi subsister sur plusieurs générations.

D’un autre côté, la niche peut aussi être vue comme le rôle qu’occupe une espèce dans un écosystème c'est-à-dire l’impact qu’elle a sur son environnement (abiotique et biotique). Cette vision a été développée par Elton (1927) qui insistait particulièrement sur le rôle des espèces dans la chaîne trophique (Figure 1.2). Par conséquent, la niche d’une espèce est soit vue comme l’enveloppe de ses besoins, soit comme l’ensemble de ses effets sur l’écosystème. Il est intéressant de noter que cette dichotomie trouve son parallèle en écologie fonctionnelle avec les traits de réponse et les traits d’effets (Lavorel & Garnier 2002).

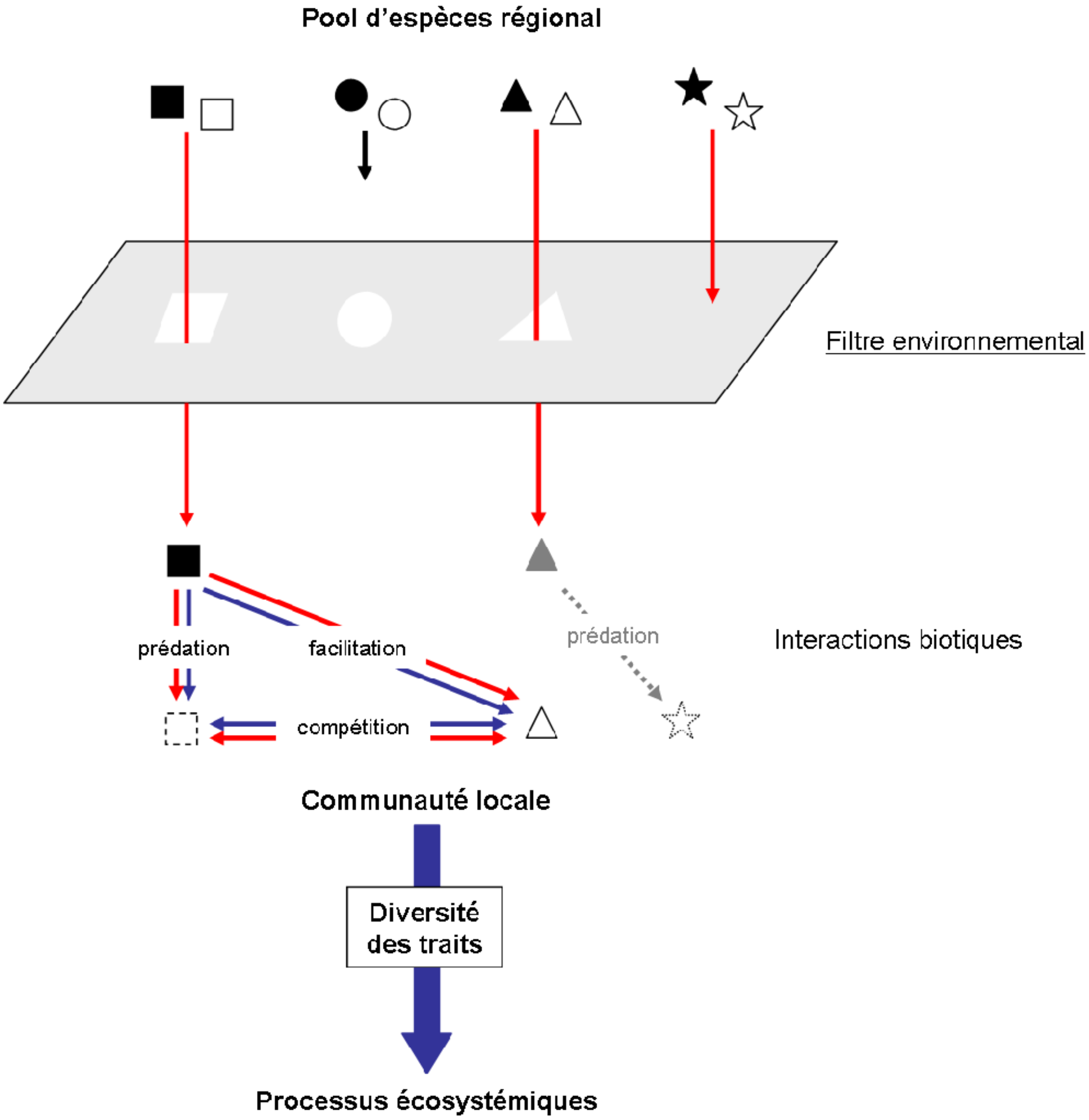

Figure 1.2. Représentation schématique des deux notions de la niche. Parmi les espèces du pool régional seules certaines passent à travers les filtres abiotiques en fonction de leurs niches environnementales respectives (symbolisées par leur forme). Les espèce représentées par des ronds sont elles limitées par leur capacité de dispersion ; elles ne peuvent donc pas atteindre un environnement qui leur était pourtant favorable. Dans la communauté locale, les interactions biotiques constituent un autre filtre. Ainsi, une espèce (triangle noir) qui ne trouve pas sa proie potentielle (l'étoile blanche) ne peut pas survivre. De même, l'espèce symbolisée par le rectangle blanc est tellement affectée par ses prédateurs (rectangle noir) et ses compétiteurs (triangle blanc) qu'elle ne peut pas persister. Au final les espèces présentes déterminent via leurs traits fonctionnels les processus écosystémiques. La niche grinnellienne regroupe les mécanismes symbolisés par les flèches en rouge alors que la niche au sens eltonien est représentée par les flèches bleues.

Par ailleurs, une autre dichotomie existe à propos de l'application de la notion de niche grinnellienne, du fait de l'ambiguïté du terme de conditions. En effet, la définition classique ne précise pas si ces conditions désignent l'ensemble de la gamme théoriquement supportée par une espèce, ou seulement celle observée in situ lorsque l'espèce est présente. Le premier cas correspond à la niche dite fondamentale alors que la seconde conception est appelée niche réalisée. Cette dernière est donc un sous ensemble de la niche fondamentale. Une illustration de cette différence est fournie par les espèces exotiques. Dans les milieux où elles ont été introduites certaines de ces espèces montrent en effet une niche écologique (variables climatiques) différente de celle observée dans leur milieu d'origine (Broennimann *et al.* 2007). Leur niche réalisée était donc, avant introduction, bien inférieure à la niche potentielle.

1.6.2. La théorie neutre

Cette théorie de la niche qui postule que la répartition des espèces est étroitement influencée par des filtres environnementaux (habitat, ressources) et biotiques (compétition, prédation) a été remise en cause par Hubbell en 2001 à travers sa théorie neutre unifiée (Unified Neutral Theory en anglais). Cette nouvelle théorie repose sur le postulat que les individus et donc les espèces sont fonctionnellement identiques (ou très proches). Leurs distributions sont alors déterminées principalement par des processus stochastiques liés à la migration et à la survie des individus. Un vif débat a fait suite à ces travaux et à leurs applications (McGill 2003, Gaston & Shown 2005, Hubbell 2005, Dornelas *et al.* 2006). Toutefois, il est indéniable que malgré sa parcimonie et son extrême simplification du vivant, la théorie neutre démontre encore sa capacité à reproduire des structures observées, que ce soit à petite (Latimer *et al.* 2005) ou grande échelle de perception (Muneepeerakul *et al.* 2008).

1.6.3 Les métacommunautés

Parallèlement à ce débat, un nouveau paradigme est apparu avec le concept de métacommunauté (Mouquet & Loreau 2002). Contrairement à la communauté qui est définie comme un ensemble d'individus en interaction directe, la métacommunauté englobe plusieurs communautés reliées entre elles par des processus de migration. Cette extension dans l'espace et dans le temps permet de mieux appréhender les effets structurant la composition des communautés. Il a ainsi été proposé quatre paradigmes synthétiques (Figure 1.3) pour expliquer les assemblages d'espèces dans les métacommunautés (Leibold *et al.* 2004).

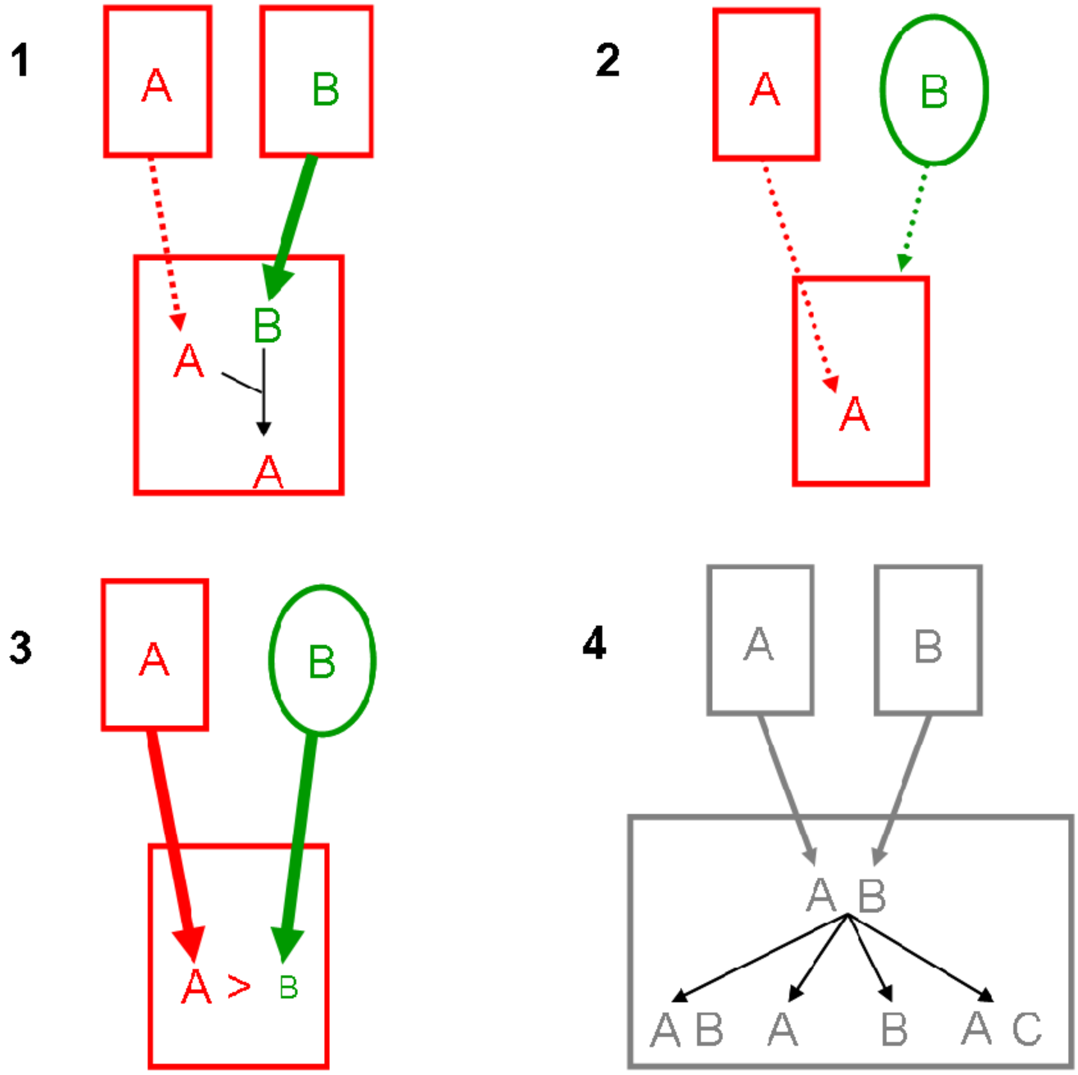

Figure 1.3. Illustration des quatre paradigmes régissant les métacommunautés. Deux espèces sont considérées (A et B), ayant chacune un habitat favorable (respectivement rectangle rouge et ellipse verte). Leurs capacités de dispersion sont proportionnelles à l'épaisseur de leurs flèches respectives. Pour chaque cas, deux communautés contenant chacune une espèce sont représentées. La troisième communauté « vide » sert de modèle pour illustrer les règles d'assemblages. (1) Dans le cas du « patch dynamic », l'espèce B a une meilleure capacité de dispersion donc elle peut occuper temporairement la communauté vacante, jusqu'à ce que l'espèce A, meilleure compétitrice ne la supplante. (2) Dans le cas du « species sorting », le filtre de l'habitat est déterminant par rapport à la dispersion et seule l'espèce A peut s'installer dans la communauté vacante. (3) A l'inverse, le « mass effect » permet à l'espèce B, disséminée en grand nombre depuis son habitat favorable de subsister dans la communauté vacante même si l'espèce A y est mieux adaptée. Enfin, si la différence entre les espèces est neutre (4), les deux espèces peuvent s'installer dans la communauté vacante. Les processus stochastiques peuvent au fil du temps mener à l'extinction d'une des deux espèces, voire à l'apparition d'une nouvelle espèce par spéciation (C).

Ces quatre paradigmes ne s'excluent pas les uns les autres et coexistent probablement suivant la structure des métacommunautés et les groupes d'espèces considérés. Ils ont surtout l'avantage de présenter un formalisme synthétique permettant de comprendre comment sont structurées les communautés.

Pour illustration, prenons le cas d'un écosystème présentant une forte variabilité environnementale, et donc des habitats très différents les uns des autres. Si les communautés sont assemblées suivant le paradigme du « species sorting » alors elles seront très différentes les unes des autres en termes de composition. Si c'est le « mass effect » qui est à l'œuvre, ces différences de composition seront moins marquées. Par contre, la distribution des abondances d'une espèce permet de discriminer les habitats « sources » (très favorables donc densément peuplés) des habitats « puits » (moins favorables mais recevant les émigrants des habitats sources). Si les différences entre espèces sont neutres, alors les communautés doivent avoir des compositions aléatoires et leur niveau de dissimilarité le sera aussi. Le « patch dynamic » peut être exclu car il n'est valable que lorsque les habitats sont similaires. Néanmoins, il est possible qu'il intervienne localement, entre les communautés et les espèces ayant les mêmes habitats, parallèlement à un « species sorting » à l'échelle globale.

En pratique, tester ces mécanismes requiert tout d'abord d'avoir un cas d'étude présentant des conditions environnementales contrastées et un nombre d'espèces suffisant. Il est alors possible de caractériser les différences dans la composition en espèces des communautés. Ceci peut se faire pour le cas simple de deux communautés via un certain nombre d'indices (Jaccard, Bray-Curtis). Plus généralement, le concept de diversité β est employé pour décrire la dissimilarité entre les communautés locales. Il quantifie le « turnover », c'est à dire le remplacement des espèces. Cette notion de diversité β est ancienne (Whittaker 1960, Lande 1996) et est employée le plus souvent pour décrire des patrons de diversité (Bryant *et al.* 2008, McKnight *et al.* 2007). Néanmoins, elle peut aussi permettre de tester les règles d'assemblage (Legendre *et al.* 2005, Anderson *et al.* 2006) et notamment de discriminer les différents types de paradigmes régissant les métacommunautés (Cottenie 2005). Toutefois, l'analyse de la diversité β reste cantonnée au nombre d'espèces partagées par plusieurs communautés alors que les autres facettes de la biodiversité β sont pour l'instant ignorées.

1.6.4 Vers une approche fonctionnelle des communautés

L’écologie des communautés s’attache à étudier la manière dont les espèces sont assemblées, mais seulement en se focalisant sur leur identité taxinomique. L’écologie fonctionnelle présente l’avantage de prendre en compte les caractéristiques biologiques des espèces afin de mieux cerner leurs effets sur les écosystèmes, mais sans réellement chercher à comprendre la dynamique et les facteurs structurant de ces communautés. C’est pourquoi McGill *et al.* (2006) ont proposé de coupler les avantages de ces deux approches et de « reconstruire l’écologie des communautés à partir des traits fonctionnels ». Ceci permet de tester des mécanismes écologiques indépendamment de la taxinomie et donc de rendre les résultats généralisables. Avec une telle approche, il est possible de passer de la classique question « dans quel conditions cette espèce vit-elle ? » à l’interrogation plus générale « quels traits sont prédominants dans telles conditions ». De même, plutôt que de chercher les facteurs influençant le nombre d’espèces présentes dans une communauté, il est plus pertinent de chercher à comprendre comment la diversité fonctionnelle est influencée par l’environnement. Cette dynamique de la diversité fonctionnelle face à la variabilité environnementale peut être étudiée de manière complémentaire à plusieurs échelles. Par exemple, au niveau régional, le long d’un gradient abiotique « naturel » mais aussi face à des changements environnementaux, et en particulier les impacts anthropiques.

Plus généralement, il est intéressant de noter que la notion de niche est particulièrement bien adaptée à l’approche fonctionnelle. Il suffit en effet de décrire chaque axe de la niche par un trait fonctionnel, la niche fonctionnelle d’une espèce étant sa position dans l’espace des traits fonctionnels (Rosenfeld 2002).Tous les concepts et applications classiques de l’écologie des communautés sont alors transposables en écologie fonctionnelle,

D’un point de vue pratique une telle approche des communautés requiert plusieurs pré-requis. Tout d’abord, étudier l’impact des conditions environnementales sur les communautés suppose que le modèle d’étude présente une assez large gamme de conditions environnementales. Ces dernières doivent en effet constituer un filtre majeur pour les espèces étudiées. Par ailleurs, les communautés doivent être suffisamment riches afin que leurs structures ne se résument pas aux interactions entre quelques espèces particulières. Les communautés doivent aussi différer fortement entre elles d’un point de vue taxinomique, sinon il est évident que leurs structures fonctionnelles seront similaires. Ces deux critères sont positivement influencés par une forte diversité spécifique à l’échelle régionale. Parallèlement, l’étude de l’impact des changements globaux sur la structure fonctionnelle des communautés requiert un système écologique suffisamment affecté et un effort d'échantillonnage conséquent pour décrire les changements de l'échelle locale à l'échelle régionale.

1.7 Les écosystèmes estuariens tropicaux : un modèle pour étudier l'effet des changements globaux sur la dynamique des différentes facettes de la biodiversité

1.7.1 Les écosystèmes aquatiques

La Terre est couramment appelée la « planète bleue » avec plus de 70% de sa surface couverte par les mers et les océans. Seule une minorité de cette surface (8,5%) correspond aux zones côtières (Constanza *et al.* 1997). Ces écosystèmes côtiers recoupent tous les climats, des zones polaires couvertes par les glaces aux zones tropicales humides ou désertiques, et toutes les conditions hydrologiques selon la topographie du plateau continental, la présence d'arrivées d'eau douces, la force des courants et l'amplitude des marées. Il n'est donc pas facile de classer objectivement ces écosystèmes et chaque classification répond en fait à une perspective. D'un point de vue écologique, c'est-à-dire en tenant compte de la diversité biologique et de la productivité, les écosystèmes côtiers remarquables sont les estuaires, les zones côtières avec une végétation aquatique dense (herbiers de phanérogames, forêts de kelp) et enfin les récifs coralliens (Constanza *et al.* 1997).

1.7.2 Les écosystèmes estuariens

D'un point de vue général les estuaires sont couramment décrits comme des écosystèmes côtiers influencés par des arrivées d'eau douce. Ces apports d'eau douce charrient aussi des minéraux et de la matière organique. Ces écosystèmes sont donc plutôt eutrophes et supportent une forte productivité (Odum 1969). Ils sont distribués tout autour du globe, dans les zones polaires (ex : mer de Kara), tempérées (ex : estuaire de la Gironde) et tropicales (ex : delta du Gange). Ils représentent 6% de la surface côtière, soit trois fois plus que les récifs coralliens.

1.7.3 Les écosystèmes estuariens tropicaux

Les écosystèmes estuariens tropicaux sont en proportion de leur surface moins étudiés que les écosystèmes coralliens. Or, ils hébergent une très forte diversité biologique et surtout fournissent des services écosystémiques de grande valeur (Constanza *et al.* 1997). Ainsi, ils jouent un rôle crucial dans le cycle des nutriments et aussi dans la fourniture de protéines via la pêche et l'aquaculture (poissons et crevettes principalement). Parmi tous les types d'écosystèmes, les écosystèmes estuariens procurent la plus grande valeur en termes de services écosystémiques (Constanza *et al.* 1997), avec plus de 22 000$ par hectare et par an (soit 10 fois plus qu'une forêt tropicale et 3,5 fois plus qu'un récif corallien)

Ils peuvent être regroupés en plusieurs types suivant leur topographie même si en réalité il existe un continuum allant des deltas aux lagunes (Blaber 2002). Tout d'abord, les estuaires ouverts sont des systèmes en permanence connectés avec la mer subissant donc l'influence des marées. Les exemples les plus connus sont l'Orénoque en Amérique du sud et le Mékong ou le Gange en Asie. Les eaux côtières influencées par les fleuves peuvent aussi être considérées comme des écosystèmes estuariens. Par exemple, l'Amazone influence la zone côtière à plus de 400 km de son embouchure. Les lagunes côtières sont à l'interface entre les décharges des fleuves et les eaux marines côtières avec lesquelles elles communiquent par des ouvertures plus ou moins larges. Les grandes lagunes tropicales sont la lagune de Terminos (Mexique) ou la lagune de Lagos (Nigéria).

Dans ces écosystèmes, les effets mixtes de deux masses d'eau contrastées induisent une forte variabilité des paramètres environnementaux, bien évidemment en termes de salinité mais aussi de turbidité, de pH et d'oxygène dissous (Basset *et al.* 2006). La partie benthique de l'écosystème est aussi très variable suivant les courants et l'exposition aux dépôts de sédiments d'origine terrestre ou marine. Les fonds vont souvent du sable grossier aux limons fins et riches en matière organique.

Cette variabilité est avant tout spatiale avec un gradient de la mer vers les eaux fluviales. Cependant, dans les régions à climat contrasté en termes de pluviométrie, la variabilité temporelle se surimpose à la variabilité spatiale. En effet, lors de la saison des pluies, le débit des fleuves augmente et par conséquent l'étendue et la magnitude de leur influence aussi. Au contraire, en saison sèche, certaines zones peu connectées avec la mer peuvent voir leur salinité dépasser les 35 psu du fait de la forte évaporation. De même, suivant les vents dominants et/ou les marées, les courants peuvent être très variables.

Cette forte variabilité spatio-temporelle des paramètres physico-chimiques se traduit aussi par une forte diversité des habitats. Les deux habitats majeurs structurés par la végétation sont les mangroves et les herbiers de phanérogames. Ainsi, le long du littoral, les racines des palétuviers offrent une zone très encombrée et peu agitée, favorisant la stabilité du sédiment et servant de nurseries à de nombreuses espèces d'invertébrés et de poissons (Primavera 1998, Nagelkerken *et al.* 2008). Les phanérogames marines poussent dans les eaux claires et peu profondes puisqu'elles ont besoin de lumière pour croitre (Orth *et al.* 2006). Elles participent fortement à la productivité primaire et constituent un refuge ou un habitat pour de nombreuses espèces qui leurs sont inféodées (hippocampe, lamantin). Les autres fonds sont nus mais leur substrat, souvent riche en matière organique, abrite une grande quantité d'organismes benthiques (annélides, mollusques).

Si les écosystèmes estuariens tropicaux ont une valeur écologique majeure, ils n'en sont pas moins fortement affectés par les changements globaux. En effet, ils sont souvent situés dans des zones très densément peuplées (ex : deltas du Gange et du Mékong) ou fortement soumises aux activités humaines notamment l'agriculture (riziculture), la pêche (crevettes, poissons) et l'aquaculture. Lorsque la population et donc la demande augmentent, ces activités requièrent de plus en plus de place et une intensification des pratiques. Ceci se fait souvent au détriment des surfaces boisées du bassin versant (mangroves près de la côte et forêts tropicales sur les bassins versants). Par conséquent la plupart des écosystèmes estuariens tropicaux ont été dégradés au cours des dernières décennies (Lotze *et al.* 2006).

1.8 Les poissons : une composante majeure du necton dans les écosystèmes aquatiques

1.8.1. Le necton : un groupe très diversifié

Dans les écosystèmes estuariens comme dans la très grande majorité des écosystèmes aquatiques, les poissons constituent une composante essentielle du necton. Le necton regroupe tous les organismes capables de se déplacer activement dans la colonne d'eau, par opposition au plancton. Il peut donc être vu comme un super-groupe fonctionnel basé sur la capacité locomotrice. Il englobe par conséquent une grande diversité d'êtres vivants, que ce soit sur le plan taxinomique ou morphologique. Le necton contient ainsi des vertébrés comme les poissons osseux, les poissons cartilagineux, les mammifères marins (cétacés, pinnipèdes et siréniens), certains oiseaux (pingouins, manchots), certains amphibiens (tritons, grenouilles) et certains reptiles (serpents de mer, iguane des Galapagos, crocodile de mer). Néanmoins de nombreux invertébrés font aussi partie du necton, notamment certains mollusques gastéropodes (lièvre de mer), des mollusques céphalopodes (poulpes, seiches, calamars), de nombreux crustacés (crabes, crevettes) et certains cnidaires comme les méduses.

Parmi le necton, il est aussi possible de distinguer les organismes benthiques, c'est-à-dire vivant principalement sur le fond (ex: pastenagues, rascasses, poissons plats), des organismes pélagiques qui se déplacent majoritairement dans la colonne d’eau (ex: anchois, thon). En réalité, il existe bien sûr un continuum entre ces deux extrêmes et, dans les écosystèmes peu profonds, de nombreuses espèces sont qualifiées de bentho-pélagiques (Froese & Pauly 2008).

Les écosystèmes estuariens tropicaux, malgré leur superficie souvent réduite, présentent une forte diversité biologique. Par exemple, le nombre d’espèces de poissons est souvent supérieur à 100 (Blaber 2002), ce qui est élevé comparativement à d’autres écosystèmes aquatiques. Ceci est à relier à la forte variabilité des conditions environnementales et la multitude des habitats disponibles. En particulier, la large gamme de salinité rencontrée dans les estuaires est une contrainte physiologique majeure. Selon leur faculté d’osmorégulation les espèces vont pouvoir tolérer une plus ou moins grande gamme de salinité et donc occuper certaines portions de l’écosystème.

1.8.2 Le necton : acteur principal des processus écosystémiques

Le necton occupe une place importante dans le réseau trophique puisqu’il contient tous les types de consommateurs, des plus bas niveaux trophiques (détritivores, brouteurs d’algues, phytoplanctonophages) aux prédateurs apicaux (orques, requins) en passant par tous les types d’omnivores. Le necton assure ainsi, via la prédation, un contrôle de type « top-down » sur les producteurs primaires comme les végétaux du benthos (Bellwood *et al.* 2006a) ou le phytoplancton (Frank *et al.* 2005). A l’inverse, les producteurs primaires influencent aussi fortement la diversité et l’abondance du necton (Ware & Thomson 2005) via la quantité de ressources disponibles (effet « bottom-up »). Ces deux types de contrôle s’exercent aussi entre les consommateurs secondaires, non seulement entre le necton et le zooplancton (Reid *et al.* 2000), mais aussi à l'intérieur du necton lui-même (Halpern *et al.* 2006).

Le necton est un acteur majeur des processus écosystémiques. Il assure en particulier le transfert et la régulation des flux de matières à travers la chaîne trophique mais aussi dans l'espace et le temps par l'intermédiaire des migrations et de la rétention des nutriments. Par exemple, les espèces migratrices de type anadromes, vivant en mer mais migrant en rivière pour se reproduire (ex: saumon), transportent des nutriments d'origine marine dans des cours d'eau relativement pauvres, contribuant ainsi fortement à la productivité primaire. A plus petite échelle, les migrations saisonnières d'adultes ou de juvéniles des estuaires vers la mer constituent aussi un important vecteur de matière organique des zones riches en nutriments vers les zones plus pauvres. Par exemple, de nombreuses espèces de poissons ou de crustacés utilisent les mangroves pour leur reproduction car elles assurent une bonne protection des juvéniles et sont riches en nourriture (Nagelkerken *et al.* 2008).

1.8.3 Les poissons, composante principale du necton dans les écosystèmes estuariens

Parmi les organismes nectoniques, les poissons (cf encadré A) constituent la majorité des espèces et de la biomasse dans les écosystèmes estuariens. La diversité en termes d'espèces se traduit aussi souvent en diversité des formes et des fonctions (régimes alimentaires, habitats, migrations). Les poissons représentent plus de la moitié des espèces de vertébrés, avec environ 30 000 espèces, dont plus de 60% sont inféodées aux eaux salées. D'un point de vue taxinomique, ces espèces sont divisées en 62 ordres et 515 familles.

Les poissons sont prépondérants pour la plupart des processus écosystémiques et constituent une part importante de l'approvisionnement en protéines des populations humaines. Ils sont ainsi activement péchés dans toutes les eaux du monde et encore plus dans les eaux côtières près des zones peuplées, en particulier dans les écosystèmes estuariens. Ces pêcheries sont souvent surexploitées et la plupart des populations sont affectées directement ou indirectement par ces prélèvements (Pauly *et al.* 1998, Dulvy *et al.* 2003). Les poissons sont aussi affectés par les autres facettes des changements globaux, notamment la destruction des habitats (ex : herbiers ou mangroves utilisés comme zones de reproduction), l'introduction d'espèces exotiques (ex : perche du Nil dans le lac Victoria) et la pollution. En conséquence, plus d'un quart des espèces marines sont actuellement menacées (Baillie *et al.* 2004, Olden *et al.* 2007).

Encadré A. Au fait, qu'est ce qu'un poisson ? Précisions phylogénétiques et sémantiques

Le titre de cet encadré, adapté du célèbre article de Wood (1957) sur les lagomorphes, souligne le fait que le mot « poisson » est largement utilisé mais recouvre en fait plusieurs définitions, chacune adaptée à un contexte. Par soucis de clarté, je vais donc préciser la terminologie qui sera utilisée dans cette thèse.

Le Littré donne comme définition du mot poisson : « Vertébré aquatique, respirant toute sa vie au moyen de branchies et pourvu de nageoires locomotrices ». Cette définition très simple reflète la vision du grand public que l'on pourrait résumer ainsi : vertébrés aquatiques ayant des nageoires et n'ayant pas de poumons (par opposition aux mammifères aquatiques). Le terme poisson est aussi largement utilisé pour désigner les poissons à nageoires rayonnées, par opposition aux requins et aux raies, et se retrouve dans la plupart des noms communs, poisson papillon, poisson volant, poisson clown…. Il est toutefois intéressant de noter que cette distinction est plus floue pour les appellations commerciales. Par exemple, la saumonette (ou roussette) est vendue comme un « poisson » sans faire référence à son statut de requin.

La volonté de classer les organismes est bien antérieure à la classification linnéenne et remonte à la Grèce antique (cf les travaux d'Aristote). Ces premières approches méthodiques des êtres vivants reposaient sur des critères simples, uniquement morpho-anatomiques et visaient des applications scientifiques mais avant tout pratiques (notamment pharmacologiques). Dans son *Histoire entière des poissons* (1558), Rondelet présente les espèces de « poissons » de Méditerranée. Ce premier livre d'ichtyologie sous-entend comme définition des « poissons », les êtres vivants aquatiques non végétaux. Rondelet y inclut les différentes familles de poissons (au sens des définitions citées ci-dessus) mais aussi des mollusques bivalves et gastéropodes (« poissons à test dur »), des mollusques céphalopodes (« poissons mous ») des crustacés (« poissons couverts de croûte »), et même des mammifères marins (cétacés et pinnipèdes). Il est particulièrement exemplaire de noter que l'hippocampe y est classé dans les « zoophytes » définis comme « les animaux marins ayant plusieurs découpures par le corps et de nature moyenne entre les plantes et les animaux ».

Encadré A. *suite*

Par ailleurs, l'ouvrage de référence *Fishes of the World* (Nelson 2006) ou le site *FishBase* (Froese et Pauly, 2008) traitent des poissons au sens des définitions du dictionnaire. D'un point de vue systématique, les poissons peuvent être divisés en cinq classes[1] (Figure A). Ces classes appartiennent toutes au phylum Chordata (*i.e.* dotés d'une chorde) et plus particulièrement au sub-phylum Craniata (i.e dotés d'un crâne) ; par opposition aux Urochordata (ascidies, salpes) et Cephalochordata (amphioxus).

Les deux premières classes sont caractérisées par l'absence de mâchoires (i.e agnathes) et regroupent les Myxini (myxines) et les Petromyzontida (lamproies). Chacune de ces deux classes ne contient qu'un ordre. Parmi les Gnathostomata (i.e doté de mâchoires), la classe des chondrychtyiens regroupe les espèces au squelette cartilagineux, avec les chimères, les requins et les raies. Il est à noter que les requins sont divisés en 9 ordres et les raies en 4 ordres (Figure A). Les Teleosteomi (*i.e.* ayant un squelette osseux) sont divisés en deux classes. D'une part les Actinopterygii caractérisés par des nageoires rayonnées sont représentés par 44 ordres. D'autre part, les Sarcopterygii possédent des nageoires lobées et sont représentés par seulement deux ordres contenant respectivement les deux espèces de cœlacanthes et les six espèces de dipneustes. Cette classe contient aussi l'ancêtre commun à tous les vertébrés tétrapodes (amphibiens, reptiles, oiseaux et mammifères). Un clade est dit monophylétique s'il. Par conséquent, les poissons ne sont pas un groupe monophylétique (*i.e.* contenant toutes les espèces issues d'un ancêtre commun), puisque sinon il faudrait y inclure tous les tétrapodes. C'est donc un groupe paraphylétique qui en pratique est souvent divisé grossièrement en : agnathes, poissons cartilagineux et poissons osseux.

Dans la suite du manuscrit, le terme poisson recoupera la définition du dictionnaire, sauf mention contraire comme par exemple dans le manuscrit A. Il est à noter que les communautés de la lagune de Terminos sur lesquelles les applications écologiques ont été menées ne contiennent que des espèces de chondrychthiens et d'actinoptérygiens.

Les poissons sont donc doublement intéressants pour étudier l'impact des changements globaux sur les écosystèmes estuariens. Ils sont en effet fortement soumis aux pressions anthropiques alors qu'ils jouent des rôles clés de par leur abondance et leur diversité. Il est donc urgent de caractériser la réponse des communautés de poissons et plus largement du necton aux changements globaux. Dans cette perspective, il est primordial de comprendre la structuration fonctionnelle des communautés de poissons dans ces environnements sous contraintes.

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[1] Selon la classification de Nelson (2006). Le présent exposé se veut synthétique et ne présente pas les clades éteints ni les incertitudes ou controverses sur la classification utilisée.

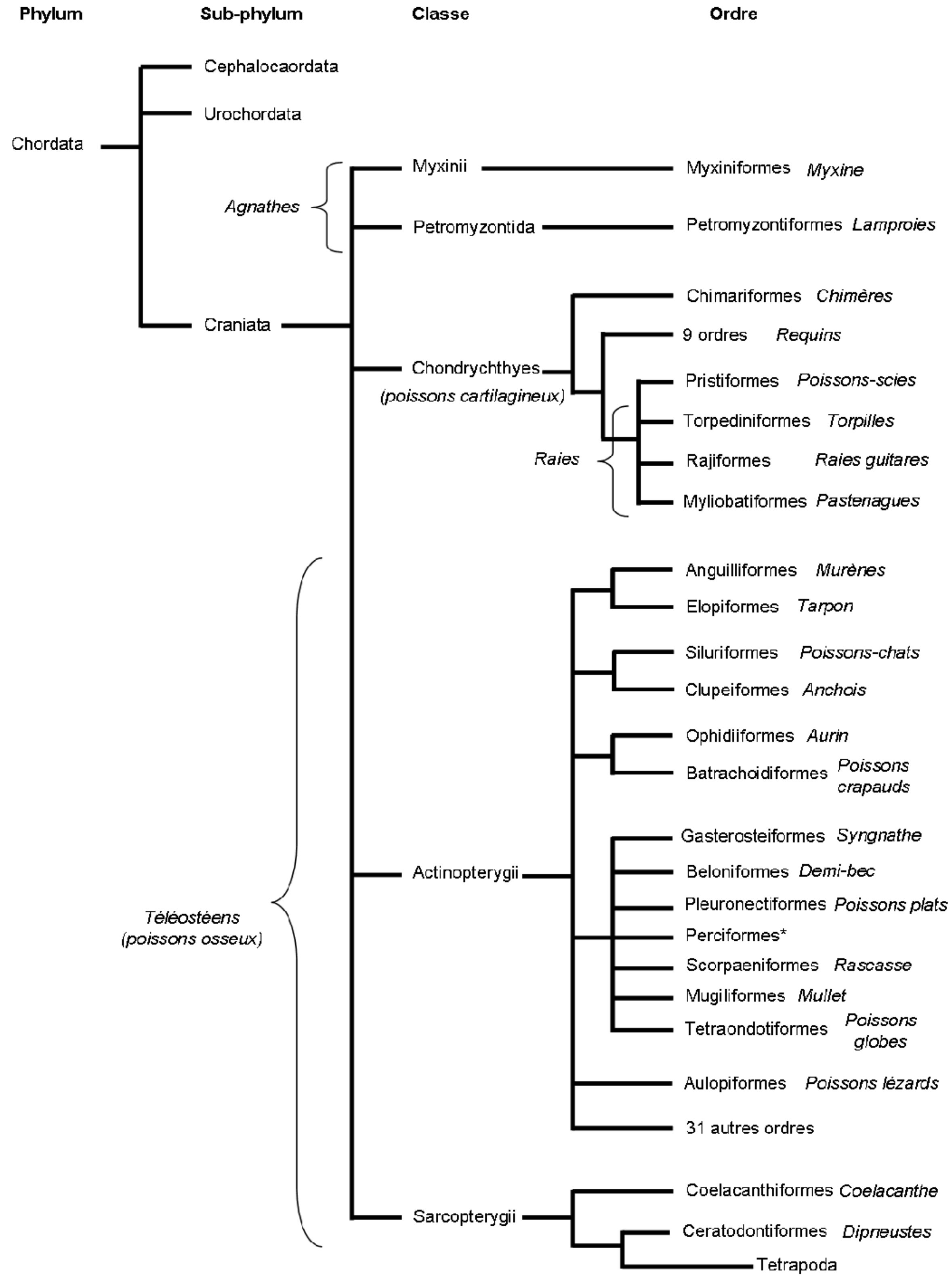

Figure A. Cladogramme simplifié des poissons. Les longueurs de branches n'ont aucune signification phylogénétique. Seuls les ordres d'actinoptérygiens présents dans les bases de données de cette thèse sont illustrés.
Pour chaque ordre, un exemple d'espèce est donné. *Les Perciformes contiennent des familles morphologiquement très différentes (cichlidés, gobies, cyprinidés).

1.9 La lagune de Terminos et sa région adjacente : un écosystème estuarien tropical sous contraintes

1.9.1 Géographie

La zone d'étude de cette thèse (Figure 1.4) se situe dans la partie sud ouest du Golfe du Mexique, le long des côtes de l'état de Campeche (Mexique). Cette région regroupe la lagune de Terminos et la partie côtière adjacente qui correspond en fait à l'estuaire du système Grijalva-Usumacinta. Le plateau continental appartient au banc de Campeche qui s'étend plus largement vers le nord et l'ouest (Figure 1.4 B). Il est caractérisé par une faible pente. La lagune de Terminos est la plus grande lagune mexicaine du Golfe du Mexique avec une superficie d'environ 1700km². La lagune est connectée aux eaux du Golfe du Mexique par l'intermédiaire de deux graus situés aux extrémités nord-est et nord-ouest, de part et d'autre de l'île de Carmen (Figure 1.4 C).

1.9.2 Climat

Le climat est tropical avec trois saisons marquées. La saison sèche s'étend de février à mai. Elle est caractérisée par des températures maximales élevées (> 30°C) et une pluviométrie quasi-nulle. La saison des pluies survient durant l'été (juin à septembre) avec des pluies quotidiennes et des températures élevées. La saison « Nortes » va de septembre à janvier et se caractérise par le passage de fronts froids et pluvieux venant du nord du Golfe du Mexique. La pluviométrie totale est en moyenne de 1800mm par an.

1.9.3 Hydrologie

La région d'étude est influencée par trois systèmes fluviaux (Figure 1.4 C) dont le débit total est supérieur à $10x10^9$ m^3 par an (Robadue *et al.* 2004). Le plus important est le système Grijalva-Usumacinta qui prend sa source au Guatemala dans les montagnes du Chiapas. Son bassin versant couvre plus de 40 000km² et c'est la deuxième plus importante source d'eau douce du Golfe du Mexique après le Mississipi. Il contribue à plus de 75% des apports dans la région. Ces apports se font via trois bras distincts : le Rio Palizada qui se jette dans la lagune de Terminos, le Rio San Pedro y Pablo et le Rio Usumacinta qui se jettent directement sur le banc de Campeche à l'ouest de la lagune.

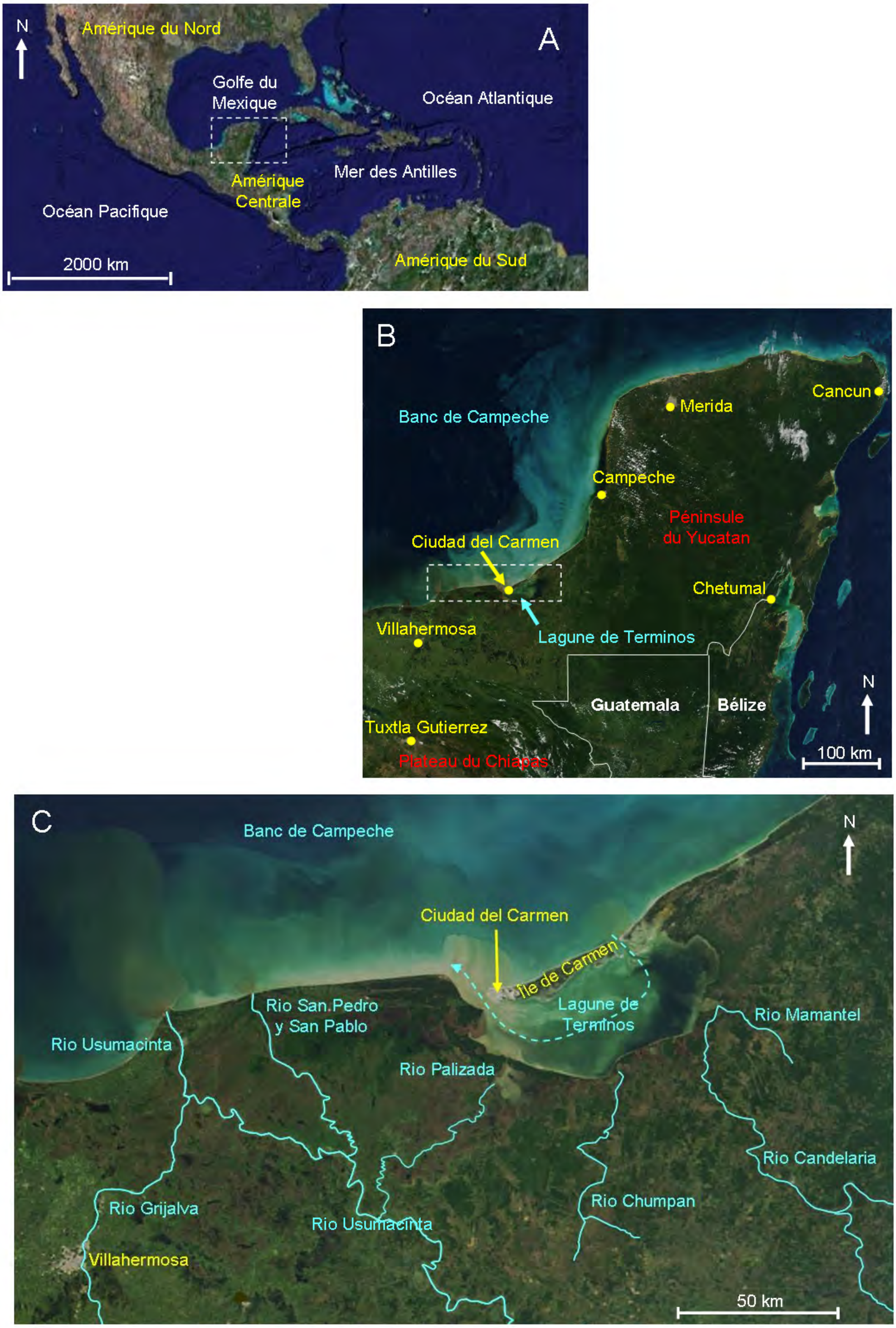

Figure 1.4. Vues satellites de la région d'étude (Images Nasa). (A) Vue générale du Golfe du Mexique. (B) Péninsule du Yucatan avec les principales villes en jaune. (C) Principaux fleuves de la région de Terminos et sens de circulation de l'eau dans la lagune (en tiretés).

Ce système fluvial, du fait de son large bassin versant situé dans les montagnes, est la principale source de sédiments terrigènes et de matière organique de la région.

Le Rio Candelaria se jette dans la partie est de la lagune au niveau de la lagune de Panlau où se jette aussi le Rio Mamantel dont l'apport est plus faible. Leur débit cumulé représente environ 20% des apports dans la région. Enfin, le Rio Chumpan se jette à l'extrémité sud de la lagune et ne contribue qu'à 5% des apports d'eau douce.

Ces apports d'eau douce sont très marqués durant la période des pluies. Le débit des fleuves devient alors très important et surtout ils charrient de grandes quantités de matériaux végétaux provenant du bassin versant. Au contraire, durant la période sèche, le débit des fleuves est plus faible et l'évaporation très forte.

La circulation de l'eau dans la lagune de Terminos est influencée par les vents dominants et suit le sens horaire (David & Kjerfve 1998). Les influences marines sont donc marquées près du grau de Puerto Real et le long de l'île de Carmen. A l'inverse, le grau de Carmen reçoit les influences des fleuves et notamment du Rio Palizada. L'eau sortant de la lagune est donc très chargée en sédiments et en matière organique d'origine fluviale et elle s'écoule le long de la côte ouest adjacente (visible sur la Figure 1.4 C).

Cette partie côtière est aussi fortement marquée par les embouchures des deux ramifications du système : Grijalva-Usumacinta, le Rio San Pablo y Pedro et le Rio Usumacinta. Les marées sont très faibles (marnage de l'ordre de 0.5m) et ont donc peu d'influence.

Comme tous les écosystèmes estuariens, la région de la lagune de Terminos présente une très forte variabilité des conditions environnementales. Par exemple, si la profondeur reste en moyenne faible (3,5m), elle peut atteindre 12m près des graus alors que les zones les plus proches de la côte sont très plates et peu profondes (<1m). La température de l'eau est toujours supérieure à 20°C avec une moyenne à 27,8°C et des maximales à plus de 32°C en été. La salinité est très variable à la fois spatialement et temporellement. Les zones influencées par les entrées marines (près du grau de Puerto Real) présentent des salinités élevées pouvant dépasser les 40psu alors que les zones près des embouchures des fleuves ont des salinités très faibles voire nulles. La transparence est en moyenne faible (distance d'extinction du disque de Secchi de 0.7m) mais est plus élevée dans les zones recevant de l'eau du large plus claire (jusqu'à 4.8m de visibilité). Cette forte variabilité spatiale due à la géographie et à l'hydrologie est encore accentuée par les variations saisonnières des conditions climatiques et notamment par le rapport entre précipitation et évaporation.

1.9.4 Sédiments

De même que les conditions hydrologiques, la sédimentologie du plateau continental reflète les influences mixtes des apports marins et fluviaux (Sanchez-Gil *et al.* 1981). La partie est de la côte est caractérisée par des sédiments sablo-limoneux carbonatés avec toutefois une étroite bande sableuse sur la façade nord de l'île de Carmen. Dans la partie ouest, recevant les apports fluviaux, les sédiments sont de type limono-argileux et riches en matière organique. Cette transition se retrouve aussi dans la lagune de Terminos.

1.9.5 Habitats

Les bords de la lagune et de la zone côtière adjacente sont couverts de mangrove et de zones humides allant des formations de type marais à des prairies humides. La mangrove est en fait constituée de plusieurs espèces, chacune adaptée à un milieu (plus ou moins inondé et plus ou moins salé). L'espèce dominante est *Rhizophora mangle* et couvre les zones littorales peu salées alors que *Laguncularia racemosa* occupe les zones baignées par les eaux salées. La mangrove joue un rôle primordial dans la productivité primaire via sa litière et elle influence très fortement les communautés aquatiques (Vargas-Maldonado et al 1981, Day *et al.* 1998).

La végétation subaquatique telle que décrite en 1980 par Yáñez-Arancibia [1] est surtout concentrée le long de l'île de Carmen à l'intérieur de la lagune, c'est-à-dire dans les eaux peu profondes et transparentes sous influences marine. Elle se compose principalement d'herbiers de phanérogames (*Thalassia testudineum*). Les herbiers jouent un rôle prédominant dans la production primaire de cette partie de la lagune (Moore & Wetzel 1982).

Des macroalgues occupent ponctuellement les fonds de type sableux sur la bordure sud de la lagune. Des bancs d'huîtres de l'espèce *Crassostreas gigas* sont présents naturellement près des embouchures des fleuves sur des portions de sédiments solides (Yáñez-Arancibia *et al.*1982).

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[1] NB : il n' y a pas eu de relevé approfondi depuis

1.9.6 Activités humaines

Cette partie du Golfe du Mexique est de plus en plus affectée par les activités humaines. Tout d'abord, la pêche à la crevette s'est fortement développée dans les années 1940 et a remplacé l'exportation de bois tropicaux comme activité principale de la région. Malgré l'effondrement successif des stocks des espèces ciblées et la chute sévère des prix, elle continue d'être une activité importante notamment autour de la ville de Carmen (au total plus de 15 000 tonnes pêchées chaque année). Cette pêche côtière est artisanale et se fait à la journée avec de petites embarcations (6-7m) et des chaluts à maille fine. Cette technique entraîne une part élevée de prises annexes non commercialisables dont une grande majorité de poissons.

L'agriculture sur le bassin versant du Grijalva-Usumacinta (Guatemala, Chiapas) est peu développée et de type vivrière (centrée sur le maïs). Sur les plaines humides près de la lagune, l'élevage extensif de bovins et la riziculture se sont développés depuis quelques années. Ces surfaces agricoles ont été gagnées aux dépens de la forêt qui recouvrait initialement ces zones. La superficie boisée est ainsi passée de 408 000 ha en 1974 à 206 000 ha en 1991 (Mas 1998). Ce développement de l'agriculture s'est accompagné de rejets de matière organique dus au bétail ainsi que de pollution par les pesticides utilisés dans la culture intensive du riz, en particulier les herbicides et les insecticides (notamment le DDT).

Depuis les années 70, le développement de l'extraction pétrolière off-shore (complexe pétrolifère de Cantarell) a entraîné un essor économique et démographique principalement concentré dans la ville de Carmen. Celle-ci a ainsi vu sa population passer de moins de 50 000 habitants en 1970 à presque 200 000 en 2005 (Cepeda 2005) et la tendance est supposée se poursuivre dans les années à venir. Cette urbanisation rapide et non planifiée s'est faite aux dépens des zones humides et de mangroves présentes sur l'île de Carmen. Les rejets d'eaux usées d'origines humaines et industrielles se font directement dans les eaux environnantes ce qui entraîne des pollutions organiques (eutrophisation, résidus carbonés de l'industrie pétrolière) et chimiques (métaux lourds).

1.9.7 Intérêt écologique

La région de la lagune de Terminos est une zone d'intérêt écologique majeure de par sa taille et sa biodiversité végétale et animale (INE 1997). En effet, elle abrite 374 espèces de végétaux et plus de 1400 espèces animales, dont 30 espèces de vertébrés endémiques et plus de 120 espèces de poissons. C'est aussi l'une des principales zones humides pour l'hivernage des oiseaux migrateurs en provenance d'Amérique du Nord. Les eaux de la lagune abritent, par ailleurs, deux espèces de mammifères marins emblématiques, le grand dauphin *Tursiops truncatus* et le lamantin *Trichechus manatus*.

1.9.8 Protection/conservation

Compte tenu de sa valeur écologique et des menaces auxquelles elle fait face la lagune de Terminos a été déclarée zone naturelle protégée (*Area de Protección de Flora y Fauna de la Laguna de Términos*) par le gouvernement fédéral du Mexique en 1994. La superficie totale de cette zone est de 700 000ha. La partie terrestre est découpée en cinq subdivisions suivant le degré de préservation et d'utilisation (INE 1997). Pour la partie aquatique, le plan de gestion prévoit une exploitation rationnelle des ressources par la pêche avec l'interdiction de pêcher dans les zones de nurseries (de poissons, d'oiseaux ou de tortues).

1.9.9 Changements observés

Les communautés piscicoles de la lagune de Terminos ont fait l'objet de nombreuses investigations depuis les années 1980. En particulier, des études ont porté sur la structure des communautés de poissons (Yáñez-Arancibia *et al.* 1980, Sosa-López *et al.* 2007), leur dynamique spatiale et les relations trophiques (Ayala-Pérez 2006). D'autres études se sont intéressées aux changements temporels survenus entre les années 1980 et la fin des années 1990. Sosa-López *et al.* (2005) ont ainsi mis en évidence de profondes modifications environnementales entre ces deux périodes avec notamment un comblement marqué (diminution de la profondeur de l'ordre d'un mètre). Ramos-Miranda *et al.* (2005) ont eux montré que les changements de composition des communautés avaient entraîné un remaniement des espèces dominantes.

1.10 Problématique de la thèse

La région de la lagune de Terminos présente donc les caractéristiques classiques des écosystèmes estuariens tropicaux avec une forte variabilité spatio-temporelle des conditions environnementales, une forte diversité biologique, et une exposition récente mais marquée aux perturbations d'origine anthropique. Les poissons constituent un compartiment majeur de la partie immergée de l'écosystème, que ce soit en termes de nombre d'espèces, de biomasse ou de valeur économique.

Des études ont déjà mis en évidence les principaux facteurs de structuration de ces communautés piscicoles et ont dégagé certaines tendances face aux modifications environnementales. Néanmoins ces études se sont focalisées sur la structure taxinomique des communautés et il est donc nécessaire d'aller plus loin en développant une approche fonctionnelle des communautés de poissons.

Cette thèse vise donc à comprendre la dynamique de la structure fonctionnelle des communautés ichtyologiques de la lagune de Terminos (Figure 1.5). Cette dynamique est appréhendée à une échelle restreinte en relation avec la forte variabilité spatio-temporelle des conditions environnementales, et à une plus large échelle temporelle en relation avec les destructions d'habitats survenues dans la lagune au cours des 20 dernières années. Pour répondre à cette problématique, il a tout d'abord été nécessaire de développer un socle méthodologique adéquat, car les outils requis n'étaient pas présents dans la littérature.

Cette réflexion théorique est divisée en deux axes faisant chacun l'objet d'un chapitre:

- Comment caractériser fonctionnellement les poissons ? Quelles fonctions biologiques devons-nous considérer et avec quels traits pouvons-nous les quantifier ? (Chapitre 2)
- Comment décrire la diversité fonctionnelle d'une communauté ? Quelles sont les facettes à prendre en compte et quels sont les indices qui peuvent les quantifier ? Comment mesurer la dissimilarité fonctionnelle entre les communautés ? (Chapitre 3)

Dans le chapitre suivant (Chapitre 4), je présente les bases de données que j'ai utilisées au cours de cette thèse, afin d'en détailler l'acquisition et les caractéristiques, et ainsi d'en fournir une vision d'ensemble au lecteur. La liste des espèces étudiées est présentée en annexe ainsi que les photos des espèces principales.

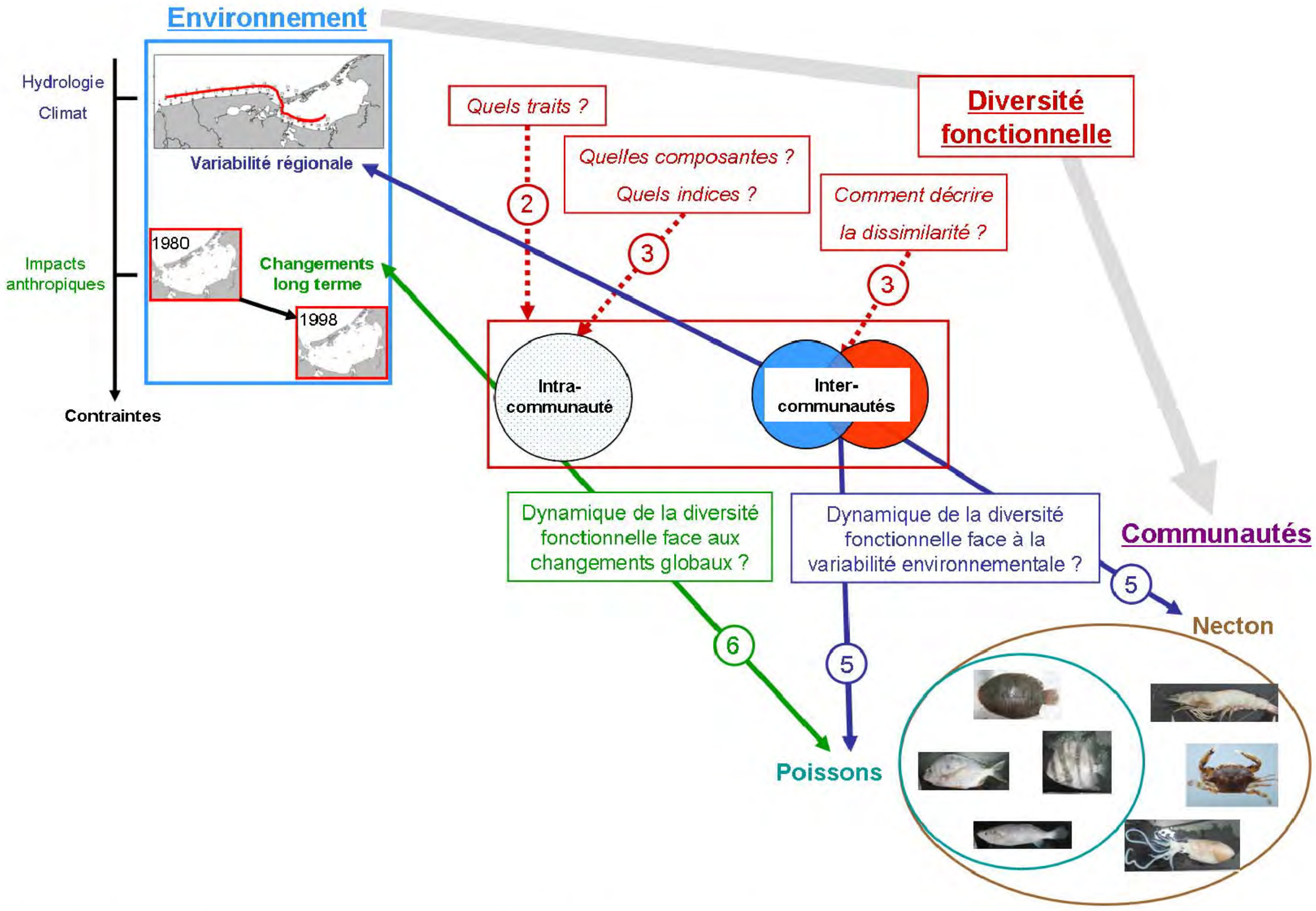

Figure 1.5. Schéma de la réflexion menée dans cette thèse. La flèche grise illustre la problématique générale. Les questions encadrées en rouge représentent les réflexions théoriques et méthodologiques. Les encadrés vert et bleus montrent les applications écologiques conduites à deux échelles temporelles : petite échelle en bleu et grande échelle en vert. Les numéros renvoient aux chapitres correspondant à chaque question.

Une fois définis les concepts théoriques et les outils d'analyses appropriés, j'ai axé les applications écologiques sur deux problématiques :

- Quelle est la dynamique spatio-temporelle de la diversité fonctionnelle des communautés de poissons? Plus largement, comment la diversité trophique des communautés nectoniques répond-t-elle aux gradients environnementaux ? (Chapitre 5)
- Quelle a été la dynamique à long terme de la diversité fonctionnelle face aux changements environnementaux survenus dans la lagune de Terminos ? (Chapitre 6)

Enfin le dernier chapitre (Chapitre 7), synthétise les concepts et résultats présentés dans les chapitres précédents et présente les perspectives à développer.

Cette thèse comporte neuf manuscrits correspondant à des publications scientifiques en anglais. Chaque chapitre commence par une synthèse en français de la (des) problématique(s) et des principaux résultats développés dans les manuscrits correspondants. Ces manuscrits sont ensuite inclus dans les chapitres.

Chapitre 2

Vers un consensus pour la caractérisation fonctionnelle des poissons

> La connaissance et considération des poissons ne pourraient par meilleur moyen être enseignées que par les différences par lesquelles les uns des autres sont distincts. (…) Puisque donc la connaissance des poissons, bonne et profitable, s'acquiert par leurs différences, il faut savoir ce qu'elles sont. Nous disons que les différences des poissons se prennent de leur vie et manière de vivre, de leurs parties, de leurs actions, de leurs mœurs et complexions. »
>
> Guillaume Rondelet, *L'Histoire entière des poissons*, 1558

Ce travail de thèse est centré sur une approche fonctionnelle des communautés de poissons. Or, à l’heure actuelle il n’existe pas de réel consensus sur la manière de mener, voire même d’initier, cette approche, contrairement à ce que l’on peut observer en écologie fonctionnelle des végétaux. En effet, il existe depuis plusieurs années un consensus sur les listes de traits fonctionnels à utiliser pour décrire les plantes (Cornelissen *et al.* 2003). Ces traits permettent de caractériser les principales fonctions des plantes (croissance, reproduction, régénération) à travers des mesures anatomiques (biomasse racinaire), morphologiques (surface spécifique des feuilles) ou physiologiques (concentration en azote des feuilles). De plus, la pertinence de ces traits, relativement simples à mesurer pour étudier des stratégies écologiques complexes en termes de compétition ou de résistance aux stress, est étayée par des études en écophysiologie (Shipley *et al.* 2005) et en écologie (Wright *et al.* 2004). Cette liste de traits a notamment permis de mettre en évidence l’effet de la composition fonctionnelle des communautés sur les propriétés écosystémiques (Garnier *et al.* 2004).

La première étape de la thèse a donc été de fixer un cadre méthodologique pour aborder la niche fonctionnelle des poissons. Pour cela il convient tout d’abord de définir les fonctions biologiques d’intérêt puis de choisir ou construire les traits fonctionnels les plus pertinents pour les décrire (Manuscrit A, Villéger *et al. in prep.*). A partir de l’analyse des processus et services écosystémiques assurés par les poissons, nous avons retenu cinq fonctions d’intérêt : l’acquisition des ressources, l’influence sur les flux de nutriments, la locomotion, la défense vis-à-vis de la prédation et la reproduction. Le comportement au sens large est traité comme une fonction transversale aux précédentes.

Pour chacune de ces fonctions, nous avons établi une courte liste de traits fonctionnels permettant de les décrire. Cette liste de traits regroupe des traits morpho-anatomiques (ex : forme de la nageoire pectorale), physiologiques (ex : excrétion de l’azote) et comportementaux (ex : migrateur). Certains traits sont mesurés quantitativement (ex : longueur relative du tube digestif) tandis que d’autres sont codés qualitativement en catégories (ex : forme des dents).

Parallèlement à cette liste de traits, nous proposons aussi une méthodologie pour la mesure des traits morpho-anatomiques, utilisant les potentialités de la photographie numérique et de l’analyse d’image. Par ailleurs, le but de cette réflexion étant d’avoir une méthodologie la plus largement applicable possible, nous avons aussi discuté des conventions à adopter pour décrire les morphologies particulières (poissons plats). Nous discutons aussi des aspects statistiques à travers l’effort d’échantillonnage et les hypothèses justifiant l’utilisation de la moyenne par espèce. Finalement, les principales applications écologiques de cette approche fonctionnelle des communautés de poissons sont présentées en insistant sur sa complémentarité avec les approches taxinomiques et phylogénétiques.

A travers cet article conceptuel nous espérons susciter l’émergence d’un consensus sur les traits fonctionnels parmi les ichtyologues. Ce consensus est un préalable indispensable pour généraliser et comparer les résultats entre les différents cas d’études.

Dans cette thèse, la dynamique de la structure fonctionnelle des communautés de poissons a été menée en se focalisant sur deux fonctions, l’acquisition des ressources et la locomotion, en utilisant certains des traits morpho-anatomiques proposés dans ce chapitre.

MAUSCRIT A

Are functional traits waterproof?

Towards a functional approach of fish communities

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En préparation

Summary

1. Functional ecology of communities is becoming a powerful approach to address major ecological issues. This framework has been widely used in plant communities, thanks to a consensus on a short list of relevant traits. On the contrary, functional studies on animal communities are still scarce and are often based on a functional group approach. However, it is clearly more appropriate to define species niches and then functional structure of communities using functional traits. Since functions performed by fish are often complex and cannot not be simply described by a couple of traits we aim to develop a functional approach of ray-finned fishes by proposing a global framework including various kinds of traits.

2. Fishes play important role in ecosystem functioning and stability all over the world. These roles are related to several biological functions such as food acquisition, nutrient cycling, locomotion, reproduction, physiological stress tolerance and defence against predation. However, despite that numerous traits have been proposed, there is still no consensus on which traits to consider and how to integer them in a general framework.

3. Therefore, for each of these functions, we propose a short list of functional traits to describe them. Traits are morphological, anatomical and physiological and are rather quantitative or qualitative. Most of these traits have already been published but we also proposed some new traits.

4. We present a methodology to measure them and especially the advantage of image processing. We also detail conventions for special morphologies and discuss statistical considerations for data analysis.

5. Finally, we illustrate how this framework could be useful in testing evolutionary convergence, disentangling assembly rules and quantifying functional diversity.

6. We aim that this paper will stimulate the emergence of a consensus on functional traits used to describe fish communities. This consensus is the first step toward meta-analyses and large ecological comparisons.

Key-words: functional diversity, ecomorphology, food acquisition, swimming, physiology, nutrient cycling, ecosystem processes, Actinopterygii

Introduction

The overall goal of ecosystem management is to sustain their ability to provide goods and services upon which human welfare depends. This has been challenging in the recent decades because ecosystems are facing ever increasing human pressures. Such human-driven disturbances to ecosystems include habitat degradation, biotic interactions (through invasion and predation) and climate change (Vitousek et al. 1997). These various impacts are greatly responsible for an increasing rate of biodiversity loss which is now widely acknowledged (e.g. Jackson 2008). Human activities are causing widespread local and regional extirpations of species and dramatic shifts in the relative abundances of remaining species (e.g. Myers & Worm 2003). In turn, these alterations of diversity and structure of communities may disrupt ecological functions performed (Diaz et al. 2006). In this global change context, several crucial questions have arisen, particularly: How does biodiversity (taxonomic, functional, phylogenetic) influence ecosystem properties? How changes in environmental conditions affect species distribution, community structure and thus ecosystem functioning?

Towards a convincing answer to these issues, the functional view of ecological communities has been continuously developing during the last decade (Tilman et al. 1997, Scherer-Lorenzen 2008). This part of functional ecology focuses on functional traits as a tool to identify how environment shapes communities and, as a feedback, how ecological communities affect ecosystem properties, such as productivity or stability (McGill et al. 2006). Functional trait definition has an evolutionary background and is defined as any biological attribute measurable at the individual level which impacts organism performance and thus fitness (Violle et al. 2007). However, if this framework is widely used for primary producers and particularly for plants, applications on animals are still scarce.

For animals, functional ecology has emerged through the concept of functional groups complementary to the guild concept. Actually, as underlined by Blondel (2003), these two terms are the two sides of the same coin. Guilds refer to resource partitioning between species in a competitive context, whereas functional groups address the effect of this partition on ecosystems processes. For instance, most of functional studies in fish ecology have focused on diet to infer impact of predation on prey or nutrient transfer (Stergiou & Karpouzi 2001, Hajisamae, Chou & Ibrahim 2003, Hoey & Bellwood 2008). Besides, invertebrates have also been investigated in an ecosystem functioning perspective, for example with the bioturbation induced by benthic organisms' movements in the sediment (Pearson 2001, François et al. 2002). For vertebrates, studies on N and P excretion rates at the individual level in relation with ecosystem properties such as primary productivity have demonstrated the strong impact of fishes on streams or lakes functioning (Taylor, Flecker & Hall 2006, McIntyre et al. 2007). Some other studies, clearly dealing with functional ecology, did not use this vocabulary and even these concepts. For example, Parr et al. (2007) studied the effect of fire on seed dispersal by ants (myrmecochory) by measuring, for several ant species, distances of seed transport by individuals. The distance could be seen as a functional trait related to seed dispersal which impacts ecosystem functioning.

Contrary to animals, functional studies on plants are numerous. This difference is probably due to several factors. First, plants are primary producers and the two most studied ecosystem processes are primary productivity and nutrient cycles (e.g. Tilman et al. 1997). Second, functional traits have a strong ecophysiological background and thus have been strongly investigated on plants (e.g. Reich et al. 1998, Shipley et al. 2005). Indeed, all plants use the same resources (water, nitrogen and carbon) to growth. Therefore, their strategy differs in the way they apportion resources, through photosynthesis and nutrient absorption, and they allocate them to organs. Third, since the end of the nineties, empirical relations have been demonstrated between some traits and plant performance (e.g. specific leaf area and relative growth rate, Garnier 1992, Shipley 2006). Following this validation, a consensus has emerged on a common list of traits to use in plant functional ecology (Weiher et al. 1999, Lavorel & Garnier 2002, Cornelissen et al. 2003).

The lag in the use of functional traits towards the study of animal communities may be explained by the complexity of functions performed by heterotrophic and mobiles organisms. Indeed, if nutrient cycling by animals has been investigated (Vanni 2002), these works focus mainly on body content and excretion rates. However, as nutrients come from very diverse sources captured in very diverse ways, critical aspects of animal impacts on ecosystem are not described by these functional approaches. On another hand, it remains highly challenging to assess trait effects on organism performances since complex functions, such as food acquisition or locomotion, are certainly driven by a combination of several traits (Gatz 1979, Winemiller 1991). As an illustration, let consider the case of two marine predators, a barracuda (*Sphyraena viridensis*) and a scorpionfish (*Scorpaena scrofa*), which are both known to feed on fishes. Nevertheless, their strategies to capture prey are very different. The barracuda is a fast accelerating fish living near the surface while the scorpionfish is an ambush predator hiding on reefs. Therefore, small fishes living in the water column (e.g. anchovies) are unlikely to be caught by a scorpionfish but more likely to be eaten by a barracuda. The reverse is also true for small fishes associated to rocky habitats (wrasses). Thus, by only considering diet composition, it is difficult to assess species interactions while functional traits aim to describe more precisely food acquisition modes and ultimately fish roles on ecosystem processes.

This simple example highlights the complexity of biological functions performed by superior organisms such as fish and the impossibility to surround them by assuming direct relationships between one trait and one function. To overcome this limitation, functional traits would better be used combination to define species functional niches (Rosenfeld 2002), similarly to the multivariate Hutchinson’s niche concept. Each trait then represents an axis of this multidimensional functional space and the functional niche of each species is related to its position in this space. The aim of this paper is thus to propose a consensual framework for the functional characterization of fish.

Ray-finned fishes (Actinopterygii), hereafter called fishes, constitute the most diverse class of vertebrate with around 27,000 species (Nelson 2006). They are present in all oceans and all continents on Earth, from small brooks or ponds to the deepest sea bottom, colonizing all habitats from bare substrates to very complex coral reefs (Froese & Pauly 2008). They have large ranges of adaptations to environmental conditions, particularly to salinity (from freshwater to hypersaline environment), current, dissolved oxygen or visibility (Evans & Claiborne 2006). They also have very contrasted diets from pure herbivores to top predators (Froese & Pauly 2008). Thus, fishes exhibit very diverse morphologies, with range size going from less than one centimeter (*Paedocypris* sp) to eight meters (*Regalecus glesne*) or more than two tons (*Mola mola*), body shape from very elongated (eels) to very compact (scorpionfish) with also particular morphology such as flatfishes (Pleuronectiformes) or seahorses (Syngnathiformes).

Fishes are the main component of nekton and thus play a key role in all aquatic ecosystems (Figure 1). The ecosystem services they generate have been reviewed by Holmlund & Hammer (1999).

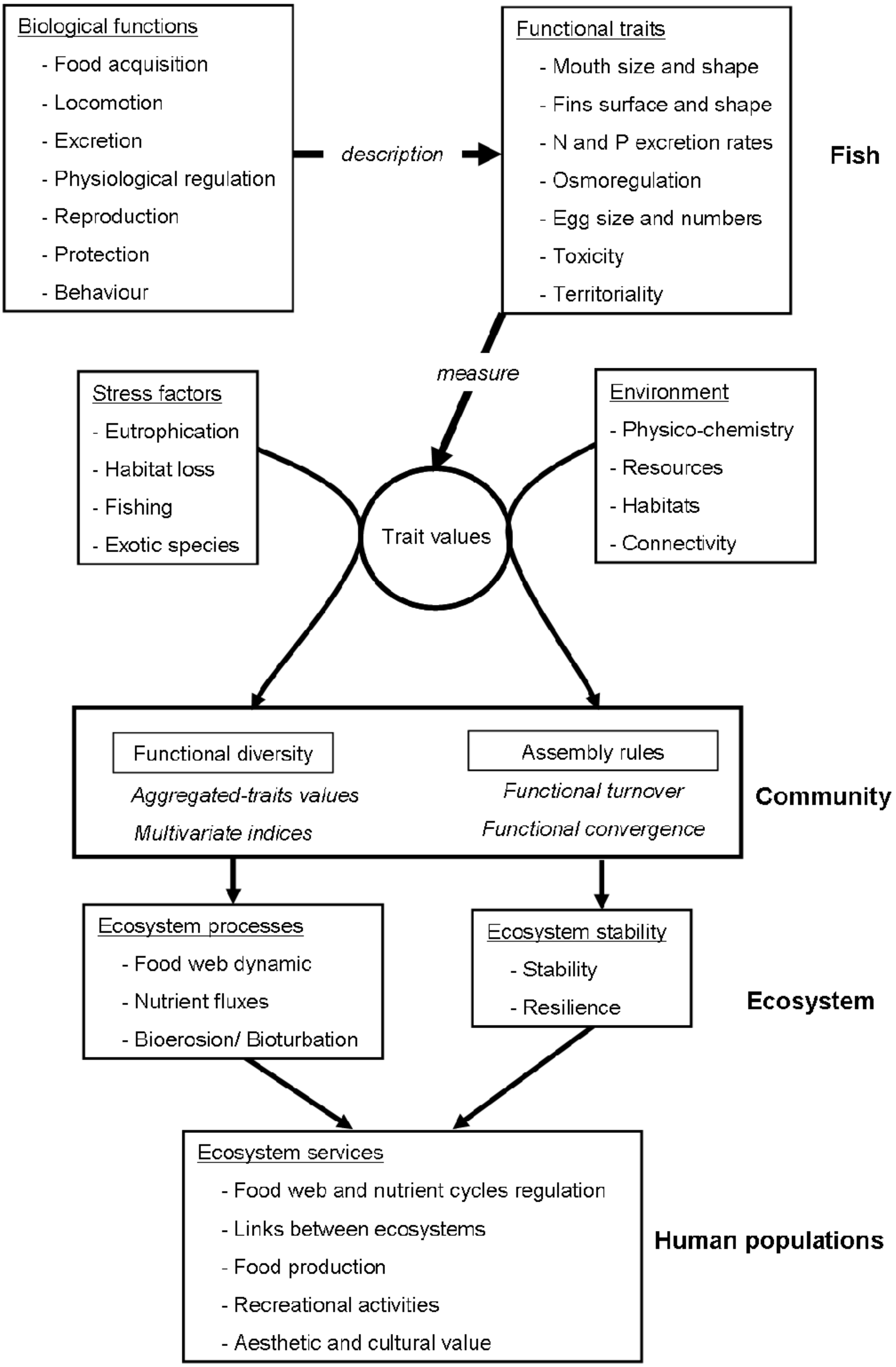


Figure 1. Framework summarizing the use of functional traits to study fish communities.

On one hand, fishes regulate food webs dynamics through their effect on their prey and predators. Theses effects may also prevent from destruction of habitats (for example fishes predating echinoid grazing corals, McClanahan 2000). They also influence nutrient cycles with top-down effect on primary producers and bioturbation of sediments (Hughes et al. 2007).

Some species also play key roles in some ecosystem processes which have profound implications on resilience and phase shift dynamic (for example the *Bolbometopon muricatum* for the bioerosion of corals reefs, Bellwood et al. 2006). Furthermore, migrating species transport huge quantities of nutrient between ecosystems and thus are active links enhancing fluxes of matter. For example salmons provide a huge quantity of nitrogen to the forest around areas where they spawn and die (up to 20 % of foliar nitrogen coming from spawning salmon, Helfield & Naiman 2001). Besides these fundamental services, fishes also provided services to human population (Figure 1), mainly as a protein supply through fishing and aquaculture (FAO 2006). They are also of cultural value as illustrated by the popularity of game fishing, aquaria and diving. Each year, ornamental fishes worth billions of dollars are traded worldwide (Pelicice & Agostinho 2005).

Most of these services are more are less closely related to two functions: food acquisition and locomotion. Actually, these two functions have been investigated in ecomorphology for several decades since the seminal papers of Gatz (1979) and Winemiller (1991). In these studies, morphological and anatomical traits are used to describe fish communities in relation to environment conditions or available resources. The number of traits used is often high and no consensus about a common list has emerged with time. On the contrary, authors tend to add new traits or to modify existing ones (e.g. Sibbing & Nagelkerke 2001). Moreover, if food acquisition and locomotion are obviously key functions performed by fishes, we believe that other aspects of fish performance such as reproduction or stress tolerance deserve to be included in a framework dealing with fish functional traits.

In this paper, we aim to provide a short list of traits contributing to define the functional niche of fishes in order to develop a functional approach of fish communities. This list of traits has to be operational and informative for all fish species and not restricted to a family or a function. Our goal is not to propose a definitive list of functional traits but rather to propose a framework for ecologists working on fish and more generally on animals. In a second part, we provide methodological considerations. Finally, we emphasize the potential of this functional approach to enhance investigations of processes underlying community assembly rules, to identify structures of fish communities along environmental gradients and to predict invasiveness.

Which set of traits for which function?

As highlighted previously, ecosystem functions performed by fish largely depend on their strategies for food acquisition and locomotion. By locomotion, we not only mean swimming performance but also fish position in the water column. Additionally to those two functions widely studied in ecomorphology, we also propose to consider nutrient cycling, reproductive strategy, defence against predation and tolerance to environmental stress as functions of interest. We will also present behaviours as transversal functions.

Food acquisition

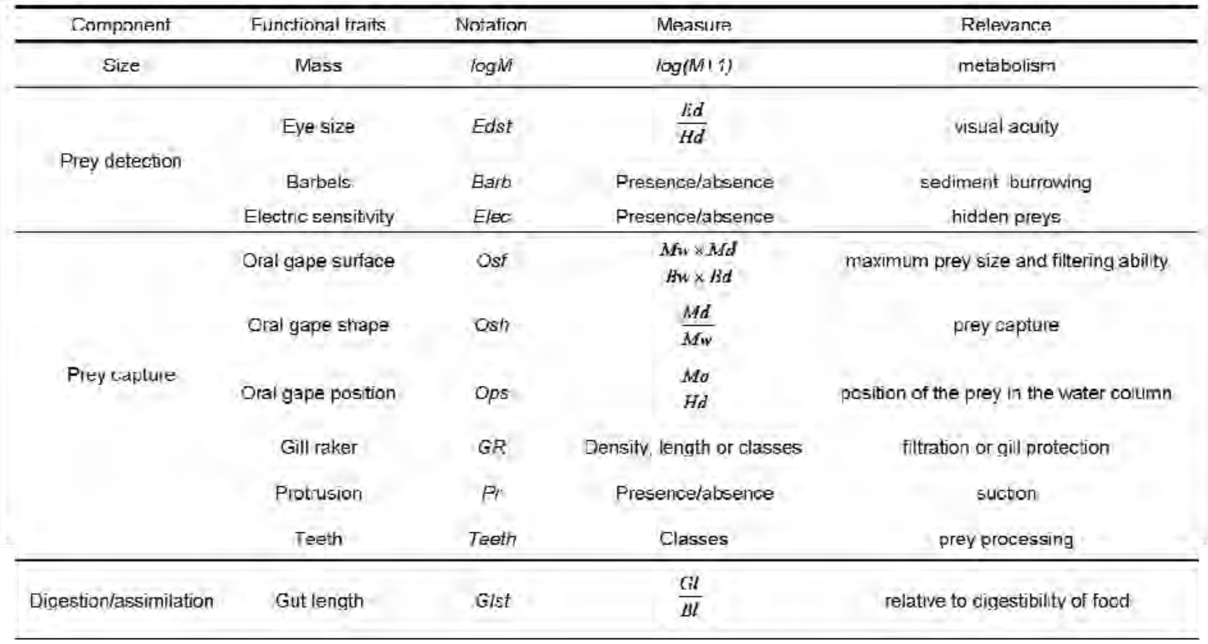
Food acquisition is a complex function involving several organs and may not, therefore, be encapsulated using one or two traits. Food acquisition goes further than diet as it also includes the way to catch food items and to assimilate them. Thus, by using relevant combinations of functional traits, we aim at going further than simply considering the mean trophic level of a species or its diet composition (Table 1).

The first component of food acquisition is fish body mass which is related to metabolism. We prefer using mass rather than standard length, despite its common use in ichthyology, because mass is more related to metabolism and trophic status than length (Akin & Winemiller 2008).

The preliminary step in the food acquisition process is prey detection (Table 1). This function is generally performed by visual stimuli. Visual acuity has been estimated by considering maximum eye diameter relatively to head size (depth at the vertical axis of eye or horizontal length from snout to opercula, Table 1, Figure 2) (Winemiller 1991, Boyle & Horn 2006). Obviously, eyesight does not only play a role in food acquisition but more generally in environment perception and particularly in detection of predators or sexual partners.

However, prey detection can also be carried out through other stimuli. For instance, some species also used barbels (e.g. catfishes, fam. Ariidae) (Gatz 1979).

Electroreception (passive) and electrogenesis (active) are also relatively common for fishes (more than 700 species, Evans & Claiborne 2006). They both allow detection of potential prey but electrogenesis involves a complex adaptation as fish produces an electric field. We advice to code the ability to detect electric field in terms of presence/absence.



Component	Functional traits	Notation	Measure	Relevance
Size	Mass	*logM*	$log(M+1)$	metabolism
Prey detection	Eye size	*Edst*	$\frac{Ed}{Hd}$	visual acuity
	Barbels	*Barb*	Presence/absence	sediment burrowing
	Electric sensitivity	*Elec*	Presence/absence	hidden preys
Prey capture	Oral gape surface	*Osf*	$\frac{Mw \times Md}{Bw \times Bd}$	maximum prey size and filtering ability
	Oral gape shape	*Osh*	$\frac{Md}{Mw}$	prey capture
	Oral gape position	*Ops*	$\frac{Mo}{Hd}$	position of the prey in the water column
	Gill raker	*GR*	Density, length or classes	filtration or gill protection
	Protrusion	*Pr*	Presence/absence	suction
	Teeth	*Teeth*	Classes	prey processing
Digestion/assimilation	Gut length	*Glst*	$\frac{Gl}{Bl}$	relative to digestibility of food

Table 1. Functional traits proposed for food acquisition description. See figure 2 for morphological measure codes. *M* represents fish body mass while *Gl* is gut length (from oesophagus to anus). See details of classes in text.

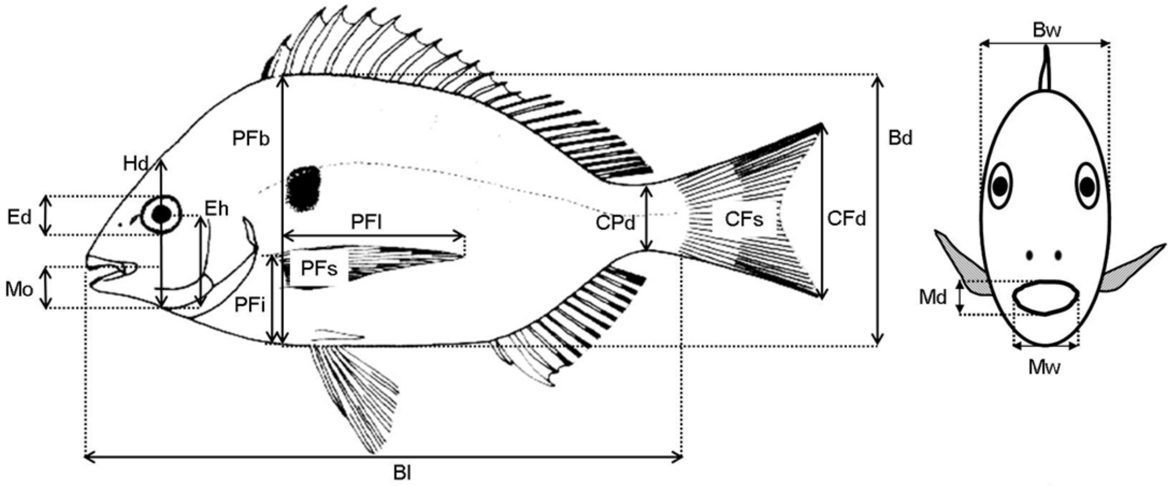


Figure2. Morphological traits measured on fish individuals. Surfaces of pectoral and caudal fins are not explicitly shown.

Once food items have been detected, the second step is prey capture. First, oral gape needs to be quantified. Ecomorphological studies often characterize shape and size of oral gapes (Gatz 1979, Karpouzi & Stergiou 2003). Oral gape shape (O_{sh}) may simply be quantified by the ratio between maximal depth (*Md*) and maximal width (*Mw*) of the mouth $O_{sh} = \frac{Md}{Mw}$ (Table 1, Figure 2). Fishes with a ratio lower than unity (i.e. vertically flattened) tend to feed on benthic organisms whereas species with higher ratio (i.e. mouth laterally flattened) tend to be filtering species (Karpouzi & Stergiou 2003).

Complementary to the shape, oral gape surface is also informative for the type of prey a fish can catch. We propose the ratio of oral gape surface to the surface of body transversal section by assuming that both are ellipsoid. Thus, the standardized oral gape surface is $O_{sf} = \frac{\Pi / 4 \times Md \times Mw}{\Pi / 4 \times Bd \times Bw} = \frac{Md \times Mw}{Bd \times Bw}$, where *Bd* and *Bw* are respectively maximal body depth and maximal body width (Figure 2). This measure is unitless.

The vertical position of oral gape is also linked to the prey position before capture and then it influences prey capture mode. Indeed, fishes with an oral gape in ventral position (e.g. Loricariidae) will tend to feed on the bottom (living prey, plants or detritus) whereas fishes with the mouth opening on the top of their head will feed near the surface (e.g. Poecilidae). Position of oral gape can be assessed by $Ops = \frac{Mo}{Hd}$ (Dumay et al. 2004),where *Hd* is head depth along the vertical axis crossing eye position while *Mo* is the vertical distance between the tip of upper jaw and the head bottom on the same axis as *Hd* (Figure 2).

The presence of protrusion may also be considered, either quantitatively with its maximal length (Gatz 1979, Barnett, Bellwood & Hoey 2006) or rather qualitatively with two categories (presence or absence). Species with a long protrusion catch prey by suction (Hulsey & Garcia de Leon 2005). Suction could also be directly quantified but it requires more complex morphological measurements (Caroll et al. 2004, Wainwright et al. 2007).

When prey have been caught, the next process is ensured by teeth. It remains difficult to quantify teeth characteristics so it appears more relevant to use functional categories based on shape; for example: absent, unicuspid, multicuspid, short conical, long conical or triangle serrated (Winemiller 1991). Tooth shape is indeed related to food processing (rasping, crushing, grasping …) and may vary across diets and even between modes of capture (Takahashi, Morivaki & Hori et al. 2007).

Similarly, gill rakers, when present, may play a role in food acquisition, especially for species filtering plankton (Tanaka, Aoki & Ohshimo 2006). Gill rakers are then assessed by their density on gill arch and by their maximal length (Gatz 1979, Sibbing & Nagelkerke 2001), or quantitatively (Winemiller 1991) by grouping them into ordinal categories (absence, short tooth-like, long and sparse, and long and comb-like).

The digestive process begins with the entrance of food items into the gut. Several organs are involved such as stomach, pancreas and intestine. Digestion and nutrient assimilation are complex functions performed by mechanical (muscular contraction of stomach) and/or chemical (enzymes and gastrointestinal microorganisms) processes. Thus, it remains challenging to find functional traits describing this step. However, it has been demonstrated that total gut length (*Gl*), from oesophagus to anus, is a robust indicator of fish ability to digest detritus and vegetal materials (Kramer & Bryant 1995). Indeed, digestibility of animal proteins is higher than plant or detritus and carnivorous species have short guts. On the contrary, the digestion of plant material or detritus requires a long intestine so that nutrients can be extracted from macromolecules and then assimilated (Cleveland & Montgomery 2003).

Nutrient content and excretion

Fish, as all organisms, ingest, store and excrete nutrients. The two main limiting nutrients for fish growth are nitrogen (N) and phosphorous (P) (Vanni 2002). It is thus primordial to quantify functionally how fish manage these two components through metabolism (Table 2). Nutrient acquisition is directly linked to diet via prey composition and thus is related to food acquisition (Vanni 2002). Nutrient content is measured as the proportion of N (or P) in dry biomass (Vanni et al. 2002).

Metabolic waste resulting from digestion and metabolism are mainly ammonium and phosphorous (Table 2). This excretion has been investigated in a functional perspective (e.g. Vanni et al. 2006). Indeed, it is relatively easy to assess individual excretion in the field (McIntyre et al. 2008). It is expressed as the mass of N and P excreted by unit of time and by unit of fish biomass and by the ratio between N and P excretion rates. The ratios between N and P for both body content and excretion rates provide complementary information and have also to be assessed (Torres & Vanni 2007).

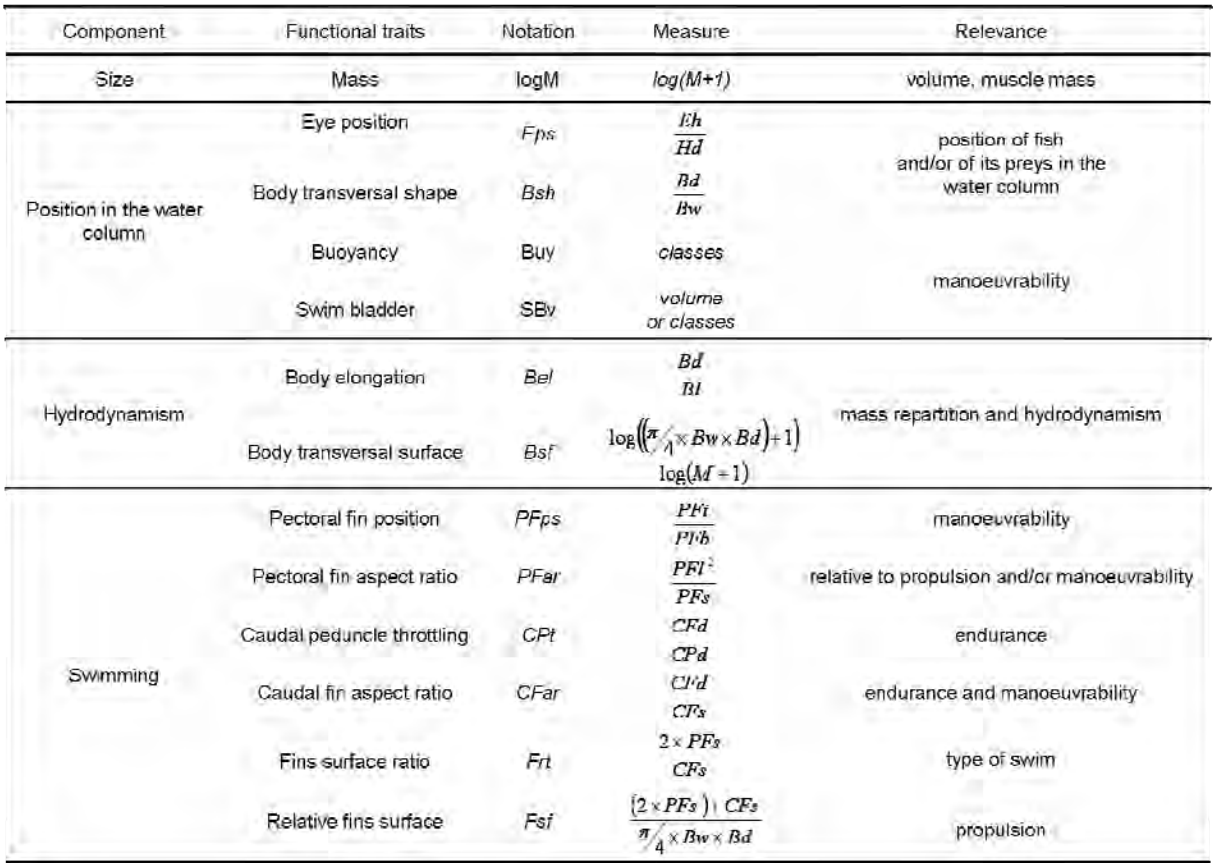
Component	Functional traits	Notation	Measure
Nutrient content	Nitrogen body concentration	*[N]*	M(N)/Mass
	Phosphorous body concentration	*[P]*	M(P)/Mass
	Nitrogen Phosphorous ratio	*[N]/[P]*	M(N)/M(P)
Nutrient excretion	Nitrogen excretion rate	*Nexc*	M(Nexc)/Mass/T
	Phosphorous excretion rate	*Pexc*	M(Pexc)/Mass/T
	N P excretion ratio	*NPexc*	M(Nexc)/M(Pexc)

Table 2. Functional traits for nutrient body content and nutrient excretion estimation. *M* represents fish body mass. The function *M()* indicates the mass of corresponding element. *T* means time

All these traits provide key information about fish functional redundancy and complementarity in terms of nutrient content and recycling. For instance, Vanni et al. (2002) found that some Loricariidae have high P concentration in their body. This is related to their bony carapace and this accumulation is allowed by their very low P excretion. More interestingly, these interspecific differences determine the level of nutrient recycling in ecosystems (McIntyre et al. 2008) and may drastically modify ecosystem structure and functioning (Taylor, Flecker & Hall 2006).

Locomotion

As pointed out before, locomotion encapsulates swimming ability and habitat use (Table 3). Swimming performance is actually involving three components (Webb 1984, Blake 2004): endurance, acceleration and manoeuvrability. Endurance is related to space occupation (e.g. pelagic species cruising all day to feed, like tuna or sailfish). Acceleration refers to the ability of fish to swim at a high speed during few seconds and will be involved either in capture of mobile prey (fish, squids…) or escapement from predators. Manoeuvrability reflects the ability of fish to make some precise moves, i.e. to swim backward and to turn quickly, thus to swim in complex environments such as reefs or vegetated areas.



Component	Functional traits	Notation	Measure	Relevance
Size	Mass	logM	*log(M+1)*	volume, muscle mass
Position in the water column	Eye position	*Fps*	$\frac{Eh}{Hd}$	position of fish and/or of its preys in the water column
	Body transversal shape	*Bsh*	$\frac{Bd}{Bw}$	
	Buoyancy	Buy	*classes*	manoeuvrability
	Swim bladder	SBv	*volume or classes*	
Hydrodynamism	Body elongation	*Bel*	$\frac{Bd}{Bl}$	mass repartition and hydrodynamism
	Body transversal surface	*Bsf*	$\frac{\log\left(\left(\pi/4 \times Bw \times Bd\right)+1\right)}{\log(M+1)}$	
Swimming	Pectoral fin position	*PFps*	$\frac{PFi}{PFb}$	manoeuvrability
	Pectoral fin aspect ratio	*PFar*	$\frac{PFl^2}{PFs}$	relative to propulsion and/or manoeuvrability
	Caudal peduncle throttling	*CPt*	$\frac{CFd}{CPd}$	endurance
	Caudal fin aspect ratio	*CFar*	$\frac{CFd}{CFs}$	endurance and manoeuvrability
	Fins surface ratio	*Frt*	$\frac{2 \times PFs}{CFs}$	type of swim
	Relative fins surface	*Fsf*	$\frac{(2 \times PFs)+CFs}{\pi/4 \times Bw \times Bd}$	propulsion

Table 3. Functional traits proposed for food acquisition description. See figure 2 for morphological measure codes. *M* represents fish body mass. See details of classes in text.

Swimming performance, as any movement in fluid, is influenced by both propulsion and hydrodynamism (Sfakiotakis, Lane & Davies 1999, Blake 2004). First, it seems obvious that size affects fish ability to swim. For example, larger fishes are expected to be faster and more enduring than small ones, because muscle biomass will be proportionally higher compared to surface friction during swimming. On the other hand, small fishes will be advantaged in three dimensional habitats with a lot of obstacles such as mangroves, seagrass beds or coral reefs.

Propulsion is ensured by fins and or/body. Fishes could be functionally classified according to their propulsion tools into two categories (Blake 2004). First, fishes that use their body and/or caudal fin (BCF) with a continuum from anguiliforms (eels, moray) to thunniforms (tuna, sailfish). At the opposite, other species use mainly median paired fins (MPF), either with rowing or flying movements. However this dichotomy is not always true and some species (e.g. Sparidae) used the two types of swimming modes, depending on conditions. For example, at low speed they will use MPF but BCF at higher speed (Blake 2004).

BCF swimmers are expected to have small pectoral fins compared to their caudal fin (thunniforms) or neither caudal fin nor pectoral fins (or very small one) (anguiliforms). Therefore, we propose to quantify the ratio (*Frt)* of pectoral fins surface (*PFs*) to caudal fin surface (*CFs*) as $Frt = \frac{2 \times PFs}{CFs}$ (Figure 2). For coherence, we argue that anguiliforms may have an *a priori* fixed value of 0 for this trait (see details below).

For MPF swimmers, the two types of fin movements, rowing or flying like, are correlated with fin shape: rowing species have relatively round fins (puffers) whereas flying ones have long fins (wrasses). Pectoral fin shape (*PFar*) is often characterized by the aspect ratio (Fulton, Bellwood & Wainwright 2001, Wainwright, Bellwood & Westneat 2002) which is $PFar = \frac{PFl^2}{PFs}$ where *PFl* is the maximal fin length (Figure 2). This index is low when fin is rounded and high when it is elongated.

Similarly, the angle of fin attachment to the body axis deserves also be taken into account since "flying" species have a more horizontal attachment than rowing species. However, Wainwright, Bellwood & Westneat (2002) suggest that this measure is well correlated to fin shape so it does not add supplementary information.

For caudal fin, there are two main characteristics that influence swimming performance (Table 3). First, the contractions of muscles located at body rear are transmitted to caudal fin by the caudal peduncle to which the caudal fin is attached. This peduncle movement generates a lateral drag which decreases swimming efficiency (Blake 2004). This is why pelagic species tend to have a very marked peduncle throttling. The peduncle throttling (*CPt*) can be easily estimated (Webb 1984) by dividing the maximal caudal fin depth (*CFd*) by caudal peduncle minimal depth (*CPd*): $CPt = \frac{CFd}{CPd}$ (Figure 2).

The efficiency of caudal fin translation is also influenced by caudal fin shape. Similarly to pectoral fins, caudal fin shape (*CFar*) is described by its aspect ratio (Gatz 1979): $CFar = \frac{CFd^2}{CFs}$.

High-endurance species tend to have crescent–like caudal fins in relation with propulsion efficiency and drag reduction. On the contrary, maneuverable species tend to have rounded fins to increase movement precision.

Body shape is of primary importance for hydrodynamism (Table 3). Indeed, swimming performance is affected by interactions between water and fish body (drag and friction). Thus, it seems necessary to compare fin surfaces, which are related to propulsion, to body transversal section which is related to water penetration. It could be achieved using the following ratio: $Fsf = \frac{(2 \times PFs) + CFs}{\frac{\pi}{4} \times Bw \times Bd}$, which postulates that body section is an ellipsoid (Figure 2).

The shape of this transversal section is also informative on fish position in the water column. Indeed, fishes swimming in the water column have laterally flattened bodies while fishes living on the substrate tend to be more cylindrical or even flat. Shape of transversal section can simply be estimated using $Bsh = \frac{Bd}{Bw}$ (Gatz 1979).

Body shape can also be assessed along the fish axis to distinguish between very elongated and very squat fishes. The elongation factor (B_{el}) is simply the ratio between maximal body depth to standard length $Bel = \frac{Bd}{Bl}$ (Gatz 1979). Additionally, to include a hydrodynamism consideration, we propose the following index to quantify relative body transversal surface: $Bsf = \frac{\ln\left(\left(\frac{\pi}{4} \times Bw \times Bd\right) + 1\right)}{\ln(Mass + 1)}$ which compares the transversal section surface to fish biomass. Elongated species have low values whereas compact species have high values.

Eye position on the vertical axis along the head is also related to fish position in the water column and/or of its prey (Winemiller 1991, Pouilly et al. 2003). For example fishes with eyes at the top of the head are often ambush predators living on the substrate (toadfishes), but can also feed near the surface for example on insects (gen. *Anablep*s).

Buoyancy is also clearly related to fish position in the water column. It could be estimated easily by considering if the fish sinks or not at a given salinity. It could also be characterized by the volume of swim bladder which is involved in the regulation of vertical position (Gatz 1979). For instance, fishes with a large swim bladder have often a high vertical manoeuvrability.

Reproduction

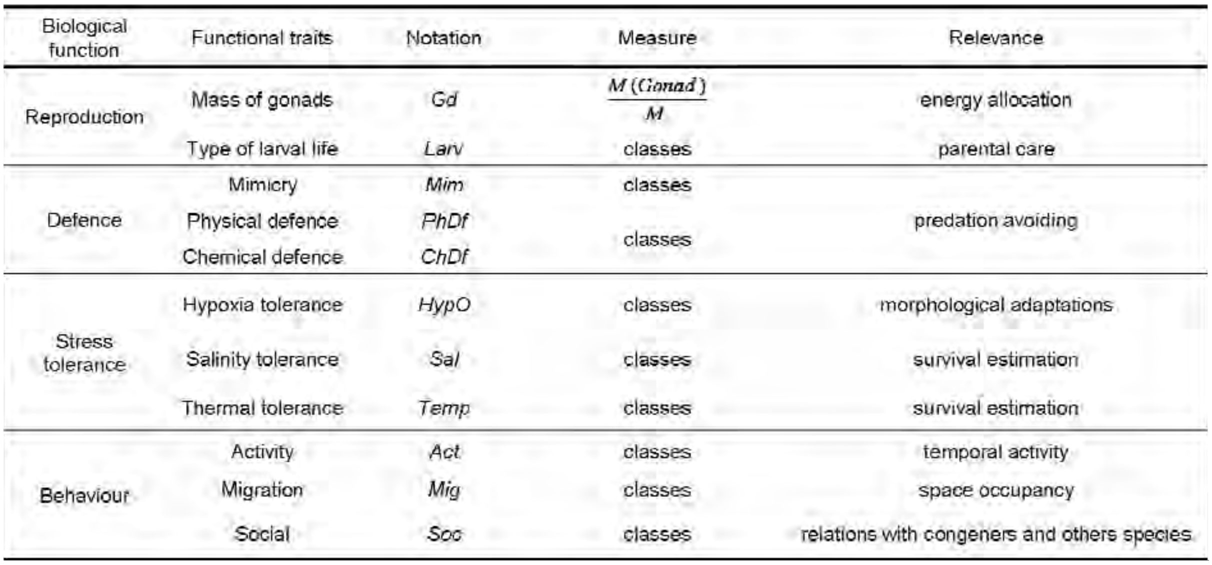
Reproduction is a critical function as it influences fish demography and thus fish effects on ecosystem processes. Since functional traits have to be defined at the individual level, we have to distinguish demographic parameters from functional traits *stricto sensu* (Table 4). For instance, the finite rate of population increase and the mean survival rate are not functional traits but demographic parameters.

On the contrary, we can quantify reproduction investment using gonad biomass. This trait has the advantage to be informative for both sexes, even if values cannot be compared between sexes, female investment being always higher than male one. Size and number of eggs are related to reproductive strategy but are relevant only in mature females (Blanck et al. 2007).

The type of larval life is also a relevant indicator for reproductive strategies and since it can be estimated on individuals it can be considered as a functional trait. We suggest to code this trait in categories such as planktonic, buccal incubation (cichlids, catfishes), or ovoviviparity (poecilids, seahorses). It will also greatly influence potential dissemination and rate of survival (Franco et al. 2008).

Tolerance to environmental stress

Aquatic ecosystems offer a high variety of environmental conditions depending on their geographical position and physical characteristics. Fishes have thus to face various physiological constraints at short time scale (seasonal migration) and during their life cycle (e.g. anadromous and catadromous species). These environmental factors act as filters and structure fish communities (Mason et al. 2007, Mouillot 2007, Mouillot et al. 2007). We thus believe that despite their complexity we have to assess these tolerances in a functional perspective. In this part, we focus on the main stressing factors that affect individual fish fitness: salinity and low dissolved oxygen (Table 4).



Biological function	Functional traits	Notation	Measure	Relevance
Reproduction	Mass of gonads	*Gd*	$\frac{M\,(Gonad)}{M}$	energy allocation
	Type of larval life	*Larv*	classes	parental care
Defence	Mimicry	*Mim*	classes	predation avoiding
	Physical defence	*PhDf*	classes	
	Chemical defence	*ChDf*		
Stress tolerance	Hypoxia tolerance	*HypO*	classes	morphological adaptations
	Salinity tolerance	*Sal*	classes	survival estimation
	Thermal tolerance	*Temp*	classes	survival estimation
Behaviour	Activity	*Act*	classes	temporal activity
	Migration	*Mig*	classes	space occupancy
	Social	*Soc*	classes	relations with congeners and others species

Table 4. Functional traits describing reproduction, defence, stress tolerance and behaviour. *M* represents fish body mass while *M(gonad)* is gonad mass. See details of classes in text.

Aquatic ecosystems can be roughly separated into two categories: fresh waters with salinity near 0 psu and marine waters with salinity near 35 psu. However, observed salinities fill the entire range between these two levels like in estuaries (e.g. Sosa-Lopez et al. 2007) while some ecosystems are characterized by hyper concentrated waters with salinity up to 90 psu (e.g. Sine Saloum inverse estuary in Senegal, Panfili et al. 2004). Ray-finned fishes are thus regulating their body fluid composition to maintain a constant osmolarity (Marshall & Grosell 2006). Consequently, when water osmolarity is lower than fish osmolarity, fishes passively loss ions and gain water. As a response, they produce an abundant dilute urine and uptake actively ions. On the contrary, in marine waters, osmolarity is higher than fish's fluid and fish tend to lose water. Thus, they drink a lot and compensate the corresponding intake of ions (mainly Na^+ and Cl^-) by active excretion. Osmoregulation is actually a very complex process involving several organs, several molecular pathways and hormonal controls (Marshall & Grosell 2006). However, for functional ecology purposes, we may consider the dichotomy between hyper-osmoregulation in freshwater and hypo-osmoregulation in salt-water. The shift corresponds to the constant fish osmolarity and is around 12 psu. Therefore, euryhaline species, i.e. living at salinities below and up to 12 psu, need to shift between hyper and hypo osmoregulation. For marine species, tolerance to high salinity depends on their capacity to maintain efficient hypo-osmoregulation when external osmolarity increase (Sangiao-Alvarellos et al. 2005).

The quantification of salinity tolerance requires complex experiments involving histological, physiological and molecular analyses. These extensive ecophysiological investigations cannot be carried out on many species. As an alternative we need more basic measures of this functional trait. Thus, to assess salinity tolerance, we may test fish survival to given levels of salinity and assign fish to categories. For example, if a fish survives between 5 and 30 psu, it is considered as a euryhaline species, if it only survives in fresh water (0-2 psu) it is a stenohaline freshwater species and finally if it only survives at 30 psu or more it is a stenohaline marine species. This measure does not assess the impact of a given level salinity on fish fitness but more modestly gives a good estimation of survival ability at this salinity level.

In the same vein tolerance to temperature can be tested from 0 to 30°C with intervals of 5°C. Indeed, except few species, fish are heterotherm and thus have their metabolism influenced by temperature. For instance, tolerance to low temperature could be an important filter for exotic species (e.g. lessepsian species in the Mediterranean Sea, Lasram et al. 2008).

Many fish species live in hypoxic waters (i.e. less saturated in O_2 than ambient air) for example when rates of oxygen consumption are high (e.g. degradation of organic matter by bacteria) and/or temperature is elevated. Those fishes have thus to adapt to this stress or to leave the environment when hypoxia occurs. Thus, fishes living in closed habitat (e.g tropical ponds or swamps) or unable to migrate, may exhibit adaptations to low oxygen levels (Graham 2006). The first type of adaptation is physiological and involves hemoglobin blood concentration and its affinity for oxygen (Wu 2002). By this way, fish are able to absorb more efficiently dissolved oxygen. Another adaptation is behavioral and consists in swimming up to the surface in order to use water oxygenated by atmospheric diffusion. This is often related to adapted morphologies with a terminal mouth and a flat dorsal face, as for example in Poeciliidae. The last strategy is very different since some fishes are able to absorb oxygen in air. Air breathing has evolved in different lineages (in 50 families representing more than 370 species, Graham 2006). Actually, air breathing encompasses several adaptations with modified epithelia (e.g. mouth, intestine), modified spaces (e.g. pharyngeal sacs) or some surfaces projecting into some chambers (e.g. labyrinth of Anabantoidei). On the contrary, some species have morphological constraints like reduced mouth and/or opercular apertures that reduce water flow near the gills (puffer or seahorses). However, theses constraints have not been studied within a functional perspective and little is known about their implication for hypoxia tolerance (Graham 2006).

Finally, we propose to classify species for hypoxia tolerance in two classes according only to the presence of morphological adaptation. Indeed, the changes of hemoglobin concentration and properties may be difficult to estimate in the field and behavioral adaptation is relatively subjective. To go further, hypoxia tolerance could be assessed by testing fish survival at low dissolved oxygen concentration in controlled experiments, as proposed previously for salinity and temperature.

Defence

Fishes are a key component of aquatic food webs and are also an important source of proteins for terrestrial animals (birds, bears). Therefore, they face a strong predation pressure all over their life cycle. It is thus important to functionally characterize their defence strategies since this functional trait may determine their fitness (Table 4).

There are several ways to avoid being predated. The first one is to not be seen by predators. This ability is directly linked to coloration and then can be classified into categories. First, some species are very colourful, like coral reef fishes or some cichlids, in relation with sexual selection and are easily seen and targeted. Besides, most of fish species exhibit light mimicry with common patterns of dark back and bright ventral face (anchovies, whitefishes) which prevent from being seen from both up and down. Other species have very specialized coloration, morphology and/or behaviour and are very well concealed. The most striking examples are sea horses (especially the leafy seadragron *Phycodurus eques*) which mimic seagrass leaves, scorpionfishes and frogfishes which are ambush predators or flatfishes that burry into the substrate. We propose to classify species roughly into three categories: colourful, “classical” colours and strong mimicry.

A different way to prevent from being predated is to be not captured by predators. The most obvious option is to escape by swimming, either rapidly or with quick turning. These abilities are directly related to swimming characteristics presented before.

The other way to avoid being predated is to be uneatable, because of physical or chemical protections. Physical protections embrace three main categories: bony carapaces (boxfishes, pipefishes), spines (porcupinefishes, catfishes, and scorpionfishes) and inflating bodies (puffer, porcupinefishes). Obviously, body size is an indirect way to avoid predation since the bigger is a fish the lower proportion of predators having a larger oral gape. Fish with chemical protections can harbour venomous spines (scorpionfishes, weeverfishes) or toxic organs (e.g. puffers with tetrodotoxin).

We think that these strategies of defence should be assessed by classifying species into 5 categories: no physical or chemical defences, bony carapaces, spiny, poisonous spines and toxic. Indeed, to our knowledge, all species with inflating bodies are also either spiny or toxic.

Behaviour

Behaviour is a transversal component which potentially affects all functions previously described. It thus deserves to be functionally assessed, at least for aspects linked to ecosystem processes (Table 4). The period of activity (i.e. nocturnal or diurnal) may play a crucial role in aquatic systems. For example, if nocturnal predators are scarce, potential prey with a nocturnal activity certainly live under a lower predation pressure than diurnal species. Similarly, gregarious species will have a different impact on ecosystem processes and stability than solitary species. We propose to code this aggregation of individuals in three categories: errant solitary (seabass, trout), couple and harem (clownfish, some cichlids) and gregarious (anchovies, some damselfishes). Gregarious species can be split into two sub-categories depending on school size (less or more than 10 individuals). Obviously, these categories are not exclusive and most fishes have different behaviours depending on their age, sex or reproductive status, so mentioned categories have to be modifies according to particular purposes.

Migration, as a determinant of fish movement between habitats, can also be categorized basically with: sedentary, daily migrations (between habitats, for example coral reefs and seagrass beds), seasonal migrations (seabream or seabass), and life-cycle migrations (anadromous and catadromous).

It could be argued that some of these behavioural traits cannot be measured at the individual level and thus should not be called “functional traits”. Indeed, a single individual cannot be, by definition, gregarious. However, we can consider that the fact to swing in a school is the realisation of a functional trait, innate or learned, that leads the fish to swim near individuals of its own species. Moreover, if migrating behaviour is usually assessed by observations at species or population levels, it could be also described on individuals with a higher precision thanks to otolith microchemistry (Campana 1999).

Indeed, otoliths are ear bones that grow continuously throughout the life of the fish. They are located within the inner ear and continuously register environments that the fish have experienced (Campana 1999). The analysis of elemental composition may reveal migratory patterns of anadromous fishes since it distinguishes freshwater, brackish water and saltwater that individuals have encountered during their life cycles (e.g. Elsdon & Gillanders 2003). In turn these chemical analyses may contribute to classify fish individuals as proposed above.

Methodological and technical considerations

The functional traits described in previous paragraphs may probably be discussed and criticized while some new traits may be proposed. In this section we thus want to precise some methodological concerns about trait design and some practical uses.

Standardization

Some functional traits are designed to estimate relative size of organs independently of individual body size. This has the advantage to produce a set of independent functional traits which are unitless and that capture the different facets of fish functional niches (Dumay et al. 2004). For example, to estimate the potential visual acuity it seems logical to consider eye size. Thus, eye diameter has been widely used as a functional trait (Sibbing & Nagelkerke 2001, Mouillot et al. 2007, Mason et al. 2008a). However, this rough measure is highly correlated to fish size since bigger fishes tend to have larger eyes than smaller ones.

Therefore, eye diameter was standardized by body standard length (e.g. Dumay et al. 2004). Nevertheless, it is obvious that there is no direct relation between eye size (and more generally head size) and whole body standard length. For instance, if we applied this standardization, the barracuda has a very low relative eye size. However this low value is due to its very elongated body while its eye is relatively big compared to its head size, and it is related to its predatory feeding mode. Finally, we suggest considering the ratio between eye diameter and head length (or head depth, Winemiller et al. 1991). Indeed, as eyes are included in head skull, their size cannot exceed head size. Through this example, it clearly appears that when proposing functional traits, standardization has to be carefully though to avoid biased or non informative values.

Trait validity

Functional traits are often ratios between two morpho-anatomical measures, particularly for shape characterization (e.g. Mason et al. 2007). However, the use of ratios is a problem when the denominator is zero. It may happen for example when an organ is absent. For example, many fish species, like eels, seahorses, or cutlassfishes, do not have a functional caudal fin (i.e. efficient for swimming). Thus, in order to characterize the peduncle caudal throttling (known to be related with endurance) we suggest considering the ratio between the depth of caudal fin and the depth of caudal peduncle instead of the inverse index (i.e. swimming factor of Olden, Poff & Bestgen 2006). Indeed, all fishes have virtually a caudal peduncle and thus when the caudal fin is absent this ratio becomes zero. On the contrary, the swimming factor is not defined when the caudal fin is absent which is not logical.

The problem of trait validity may be even more complex when both the numerator and denominator have a zero value because their ratio is then undetermined. For instance, the aspect ratio is used to describe the shape of caudal fin by dividing the square of caudal fin depth by its surface (e.g. Wainwright, Bellwood & Westneat 2002). Thus, when the caudal fin is absent both its depth and surface do not make sense. Therefore the value of this undetermined ratio has to be fixed arbitrary under biological assumptions. For instance, in the case of caudal fin aspect ratio, it is hypothesized that the greater it is, the more the fish is enduring (Webb 1984). Thus a fish without caudal fin has probably a weak enduring ability and then deserves a score of 0. Therefore there is a logical continuity between species as this arbitrary zero value is actually close to that obtained for a fish with a very elongated caudal fin (low depth but high surface) such as some gobies.

Conventions for particular morphologies

Beyond mathematical consideration, practical traits have to be available for all fish species. However, as previously emphasized, fishes exhibit very diverse morphologies. The most striking examples are Pleuronectiforms (flatfishes) with their body lateralization. Thus, when focusing on functional traits, a question which arises is how do we have to consider them? For example, if we want to assess their body shape, what is the body depth of flatfish? Do we have to measure it using morphological top and bottom of the body, defined by the respective positions of dorsal and anal fins, or, at the opposite, do we have to consider fish position in the water and measure body depth accordingly? We believe that we absolutely need to choose the second option in a functional perspective and thus to measure body depth along the segment between the two pectoral fins. Given this convention, flatfishes will have a body shape similar to other vertically flattened fishes such as batfishes (Ogocephalidae) rather than similar to typical fish laterally flattened like Perciforms which is very logical on a functional point of view.

On the contrary, when looking at the caudal fin throttling of flatfishes (ratio between caudal fin depth and caudal peduncle depth), we need to consider mechanistic constrains. Indeed, despite the lateralization, the caudal fin movement of flatfishes is also induced by the caudal peduncle and is independent from the fish position. Thus, the depth of caudal peduncle has to be measured on the same plan as the caudal fin surface (i.e. horizontally when considering the flatfish lying on the substrate).

Therefore, establishing conventions to generalize the use of functional traits to particular morphologies have to be driven by biological knowledge on morphology and behaviour in order to be informative within a functional perspective.

Ontogenic changes

Among fishes, many species exhibit ontogenic changes through development. This is linked to size constrains. For example, a juvenile top predator cannot eat fishes since it measures only few centimetres long, and thus will often eat some small crustaceans and molluscs instead. Besides this example, some other species drastically change their diet between juvenile and adult phases. For example, the juvenile salema (*Sarpa salpa*) eat small crustaceans while adults are pure herbivores (sea grasses and epiphytic seaweeds) (Froese & Pauly 2008). Thus, it is expected that juveniles and adults strongly differ, at least for functional traits linked to digestion. Ontogenic changes may also deeply modify morphology, particularly between larval and juvenile stages for species that passively disperse thanks to marine currents (e.g eels leptocephalus). Therefore, for species known to have strong functional difference between life stages or sex, the traits have to be estimated on each of the stages as if they were distinct functional entities. Under this functional perspective, taxonomic considerations do not matter since we focus on individual groups acting in a similar way in aquatic ecosystems.

Which and how many individuals?

When studying communities, functional trait values at the species level have to be representative of individuals composing the community. For example, if the large majority of individuals are juveniles for a given species then functional traits have to be measured (or extracted from bibliography) on juveniles rather than on a pool containing all life stages, or worse only adults.

Ideally, functional ecology is taxonomy free and traits should be measured on all individuals of a given community we want to describe exhaustively. The measure of traits at the species level is just a practical method to save time and money under the assumption that intraspecific variations are negligible compared to interspecific ones (Dumay et al. 2004). However, this assumption does not hold when considering different stages and thus may lead to biased results. Another reason to adopt the species centred approach in functional ecology is that it allows connecting functional, demographical and evolutionary issues (Sibbing & Nagelkerke 2001, Bellwood et al. 2002, Mason et al. 2008a). In case of weak differences between sexes and the capture of individuals belonging to the same life stage, we suggest to measure functional traits on at least ten individuals by species (or stages, sex,…) and then to consider the average value over all individuals. This arbitrary sample size appears as a trade-off between cost of measurement and precision.

Practical measurement of anatomical traits

Fishes are three dimensional soft, moist and often slippery objects and are thus not easily handled. Therefore, we suggest using as often as possible digital pictures and digital processing softwares to estimate morphological measures and especially those taken from lateral profiles (Figure 2). The only precaution is that pictures do not have deformation or distortion.

This protocol is relatively convenient while allowing easily estimation of surfaces and angles. Moreover, it is easier to draw a segment on a screen using softwares (such as ImageJ) than to use a rule on a moist fish. Additionally, once pictures have been stored, it is possible to measure any new trait. This protocol can be used to measure most of morphological traits previously presented, except those related to oral gape and body width.

Some measures are theoretically objective but may be partially subjective in practice. Indeed, most of organs or body parts are soft and articulated. Therefore, it is often difficult to assess what is their ‘natural’ size. For example, traits related to fins have to be measured on spread fins. Thus, when measuring these traits, fins have to be spread to their maximal extension but without forcing (i.e. without involving membrane elasticity that link the rays). In addition, some of organs such as fins are fragile and do not have to be torn.

The general state of fishes depends mainly on sampling method. For example, rotenone poisoning or electric fishing allow capturing fishes with precaution. On the contrary, trawling may induce injuries because of frictions with the net and other fishes or organisms. Fish conservation between sampling and trait measuring is also a critical step. We suggest to freeze individuals rather than to fix them in formaldehyde. Indeed, fixation is clearly a problem for measurement of mobile parts (oral gape or fins) while after defrosting, fishes are often in a good state.

From functional traits to functional ecology of fishes

Analysing trait correlations in an evolutionary perspective

As underlined by Keddy (1992), the matrix of functional traits for a set of species can be used in two complementary ways. First, comparisons of trait values among species allow testing whether there are some correlations which may suggest evolutionary trade-offs (Collar, Wainwright & Alfaro 2007). Obviously, these correlations have an ecological meaning only if traits are not trivially correlated (e.g. because of size factor). In the list of traits proposed before, there is no such correlation. Another limit to these analyses is that the set of species have to be diverse enough to prevent from biased conclusions. Indeed, if for example the species studied come from a particular habitat, belong to the same family or have the same type of diet; correlations may be true only for this sub-sample of species. We hope that, similarly to plant functional ecology, a consensus on traits to use will quickly emerge and that in few years meta-analysis on several hundreds of species from all ecosystems will be possible.

Second, the functional matrix also allows exploring species convergence or divergence, particularly in combination with taxonomical or phylogenetical data (e.g. Winemiller et al. 1995, Winemiller & Adite 1997, Ruber, Verheyen & Meyer 1999, Wainwright 2007). At first sight, it may seem obvious that as functional traits are mainly derived from morphological traits, they will follow taxonomy. However, if this assumption is true between orders (for example, between pleuronectiforms and perciforms), it does not hold anymore when considering lower taxonomical levels (e.g. cichlids Albertson, Streelman, & Kocher 2003). Indeed, species from the same family may be functionally very different. For example Sparidae gathers herbivorous species like *Salpa salpa,* zooplanktonivorous species such as *Boops boops* and carnivorous species like *Dentex dentex*. On the contrary, functional convergence of species phylogenetically different but with similar habitats or diets may be observed (durophageous Sciaenidae, Haemulidae and Carangidae, Grubich 2003). These simple examples underline that functional approach goes really further than the simple taxonomic composition of communities.

Are functional traits really correlated to diet?

A more sensitive question is the link between diet and functional traits. Indeed, for several decades, most of studies have sought a relation between morphology and diet in order to infer fish diets from some morphological attributes (Gatz 1979, Hugueny & Pouilly 1999, Pouilly et al. 2003, Ibanez et al. 2007). Ecomorphological traits have also been used as indicator of diet in trophic studies. For instance, gut length accurately distinguishes algivores, detritivores and herbivores from carnivores (Kramer & Bryant 1995, Ward-Campbell, Beamish & Kongchaiya 2005).

Analyzing the diet of a fish species is a very hard and time consuming work, as it is necessary to estimate gut contents on many individuals. Other methods are available to estimate trophic status (C/N isotopes ratio, ecotrophic models) but they may lead to a loss of information. For instance, knowing that a species have a low trophic level (i.e. consume primary production) does not tell us if this species eats phytoplankton (anchovy), algae (parrot fishes) or detritus (mullet).

It is thus relevant to try indirect ways to estimate species diet but ecomorphology seems far from reaching a consensus since most of studies found weak relationships between diet and morphology (e.g. Ibanez et al. 2007). More precisely, Bellwood et al. (2006) demonstrated that functional specialization of oral gape and jaw morphology is not related to specialization in terms of food items ingested. This versatility has been found on labrid species with very specialized morphologies living on coral reefs. Therefore, as coral reefs are ecosystems where resources are expected to be stable through space and time, we think that this pattern will probably be true in most of ecosystems.

In addition, we argue that a common error is due to extrapolation of relations between the consumption of a food item and trait values that are demonstrated on a low number of species. For example, it has been demonstrated that gill rakers are relatively longer in species filtering water for plankton feeding (for example anchovies) (Tanaka, Aoki & Ohshimo 2006). Thus, gill raker is often used as an indicator of ability to filter water (e.g. Dumay et al. 2004). However, when examining a very large range of fishes, it quickly appears that some species may have long gill rakers, such as sea trout (*Cynocion sp*), while they are predators of crustaceans and fishes. In this case gill rakers are probably a tool to protect fragile gills from injuries caused by hard pieces (crushed shells, spines, bones). To resume, all filtering fishes have long gill rakers but the presence of long gill raker do not always indicate a filtering strategy. Such asymmetric assumptions must be carefully taken into account before linking traits and diets. As an alternative we suggest that trait combinations may provide strong relations between morphology and diet, if any.

This challenging issue raises key questions. Which functional traits do we need to optimally assess fish diet? How much variation in fish diet this trait combination can explain? If the best set of traits explains a high proportion of fish diet then functional traits will be regarded as a surrogate for fish diet composition. Then, studies dealing with trophic modelling with many species with unknown diets (like in tropical ecosystems) will benefit such proxies. On the contrary, if versatility is really high for most of species, we would conclude to an unpredictability of fish diets from traits. It would indicate a distortion between fish potential functionally niche (defined by traits) and fish realized trophic niche (observed items eaten). This difference would be driven by local food availability and fish behaviour (level of opportunism or memory of past experience) (Bellwood et al. 2006).

Testing community assembly rules based on traits

The fundamental idea behind the study of biodiversity patterns is the presumed connection between the shape of species assemblages and the functional ways in which they are organized. Hence, functional traits may provide a more quantitative and predictive way of studying community assembly rules (McGill et al. 2006) (Figure 1). For instance it is widely acknowledged that local species richness is regulated by both abiotic filters and biotic interactions. The niche filtering hypothesis assumes that coexisting species are more similar to one another because habitats (or local conditions) act as a filter, allowing only a narrow spectrum of species to survive while species with well non-adapted traits are likely to be absent (Zobel 1997). Biotic interactions are also restricting local species richness since species are in competition and the magnitude of this competition is greater between those species which share similar traits following the limiting similarity principle (MacArthur & Levins 1967).

We argue that functional traits may contribute to disentangle these various forces shaping fish communities. For example Mason et al. (2008b) used ecomorphological traits to demonstrate that pairs of abundant species tended to have relatively low niche overlap, while rare species tended to have relatively high niche overlap with abundant species. This study supports biotic interactions and niche complementarity as main factors explaining community structures in lacustrine fish communities. Tedesco & Hugueny (2006) demonstrated, using fish communities inhabiting West African tropical rivers, that the composition of fish assemblages at the drainage basin scale can be partly explained by the relationships between life history strategies and seasonality gradients in hydrological systems. Their study supports the selection of certain trait combinations due to river hydrological variability which acts as a trait filter.

Villéger et al. (unpublished manuscript) use functional traits to study the functional turnover between tropical estuarine fish communities. They partitioned functional diversity between alpha, beta and gamma component by analogy with the classical framework used on taxonomic diversity. They found a very low functional turnover despite a very strong species turnover, in relation with the strong environmental heterogeneity. Thus, species turnover is not random but functionally equivalent species tend to replace each other along the environmental gradient according to their environmental preferendum.

Functional ecology based on functional traits is clearly a promising tool to understand fish community assembly rules and the use of traits in community ecology is still in its infancy.

Analyzing fish response to environmental constrains and changes

Once functional convergence or divergence between species has been shown based on trait values; the further step is to investigate link between functional traits and environment conditions (Figure 1). The question is then, how trait values are related to a given set of environmental variables? For example, Fulton & Bellwood (2004) show different pectoral fin morphologies between labrid species living inside lagoons and on the outer slope of reefs, in relation with wave strength. Similarly, within the global changes context, it appears relevant to study fish response to perturbations in a functional perspective. Indeed, fishes, as all living organisms, are facing an increasing pressure due to disturbances be they direct (fishing, destruction of habitats) or indirect (invasive species, warming, eutrophication) (e.g. Jackson 2008). It is thus important to shift from a species centred to a traits based approach. In other words, instead of focusing on species responses, we need to investigate combinations of traits that discriminate winners and losers species after environmental changes. For instance, Olden et al. (2006) found that life-history attributes predict which native fish species in the Colorado river basin are declining either because they suffer from strong life-history overlap with exotic species (evidence for biotic interactions) or because they have life-history traits that are not well adapted to modified environmental conditions (evidence for environmental filter). One step further, Olden et al. (2008) demonstrated that species sharing particular sets of traits, some acting in concert, are going to rarity, extirpation, and extinction.

Similarly, instead of evaluating changes of the species richness of communities, it would be more relevant to study changes in terms of functional structure (Figure 1). For instance Villéger et al. (unpublished manuscript) analyzed long term temporal changes that occurred in fish communities of the Terminos lagoon (Mexico) by estimating three components of functional diversity (Villéger et al. 2008) and functional specialization. They found a loss of functional diversity and functional specialization in fish communities associated to seagrass areas while species richness was increasing. The decrease of dominance of some original functional identities was correlated with the partial destruction of seagrass beds. On the opposite, new dominant species were functionally similar to already present ones increasing redundancy and thus decreasing functional diversity. This clearly indicates that the functional approach is more informative than rather considering species composition and may become predictive.

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Chapitre 3

Comment décrire la diversité fonctionnelle des communautés ?

> The term ‘biodiversity’ is a simple contraction of ‘biological diversity’, and at first sight the concept is simple too: biodiversity is the sum total of all biotic variation from the level of genes to ecosystems. The challenge comes in measuring such a broad concept in ways that are useful.
>
> Purvis & Hector 2000

3.1 D’une diversité des groupes fonctionnels à une diversité des traits fonctionnels

La notion de diversité fonctionnelle et ses applications sont relativement récentes comparées aux autres champs disciplinaires de l’écologie. Il est intéressant de noter qu’à l’origine elle était dissociée du concept de trait fonctionnel. En effet, le premier indice de diversité fonctionnel était tout simplement le nombre de groupes fonctionnels, ces derniers étant définis a priori suivant la biologie des espèces (Lavorel *et al.* 1997). Par exemple, les végétaux herbacés étaient classiquement séparés en graminées, légumineuses, dicotylédones non légumineuses et ligneuses (Tilman *et al.* 1997). Cette classification simpliste peut s’avérer utile mais n’est pas sans défauts. En effet, toutes les espèces appartenant à un groupe sont supposées identiques, ce qui est rarement le cas, notamment en terme de cycle de vie ou de capacité compétitrice. Cette approche a donc fait l’objet de critiques car ces regroupements entraînent une perte d’information (Fonseca & Ganade 2001) et la définition relativement arbitraire des groupes peut fortement influencer les conclusions (Wright *et al.* 2006).

Parallèlement, les traits fonctionnels, définis comme des caractéristiques biologiques individuelles influençant la performance (Violle *et al.* 2007), ont été largement utilisés pour lier la composition d’une communauté aux processus écosystémiques qu’elle assure. En pratique, la communauté est souvent décrite par des traits agrégés, c’est à dire la moyenne pondérée par les abondances des valeurs de traits des espèces présentes. Cette valeur moyenne est informative et explique dans certains cas les processus écosystémiques (Garnier *et al.* 2004). Par exemple, dans les communautés herbacées, la valeur agrégée de la teneur en azote des feuilles est fortement corrélée à la productivité primaire relative. Néanmoins, il est rapidement apparu complémentaire de développer des indices pour décrire plus précisément la diversité et non plus simplement la moyenne de ces valeurs de traits. En effet, la moyenne pondérée synthétise les valeurs de traits présentes en accordant plus de poids aux espèces les plus abondantes mais elle ne permet pas de considérer la variabilité des valeurs de traits. Prenons le cas simple d’une communauté ayant seulement deux espèces, d’abondances égales et étudiées pour un seul trait. Deux valeurs similaires de traits agrégés peuvent alors correspondre à deux cas totalement différents. Dans un cas les deux espèces ont des valeurs de traits similaires mais dans un autre cas les deux espèces sont très différentes fonctionnellement et la valeur moyenne correspond à une hypothétique espèce intermédiaire.

Par conséquent, la valeur moyenne résume l'information mais ce faisant fait perdre la notion de variabilité. Elle n'est donc pas suffisante pour décrire la structure fonctionnelle des communautés. Mesurer la diversité fonctionnelle requiert donc de considérer toutes les facettes de la diversité des traits (Tilman *et al.* 2001).

3.2 D'une approche univariée à une approche multivariée

Le premier indice de diversité fonctionnelle utilisant les valeurs de traits fût proposé en 1999 (FAD de Walker) (Figure 3.1).

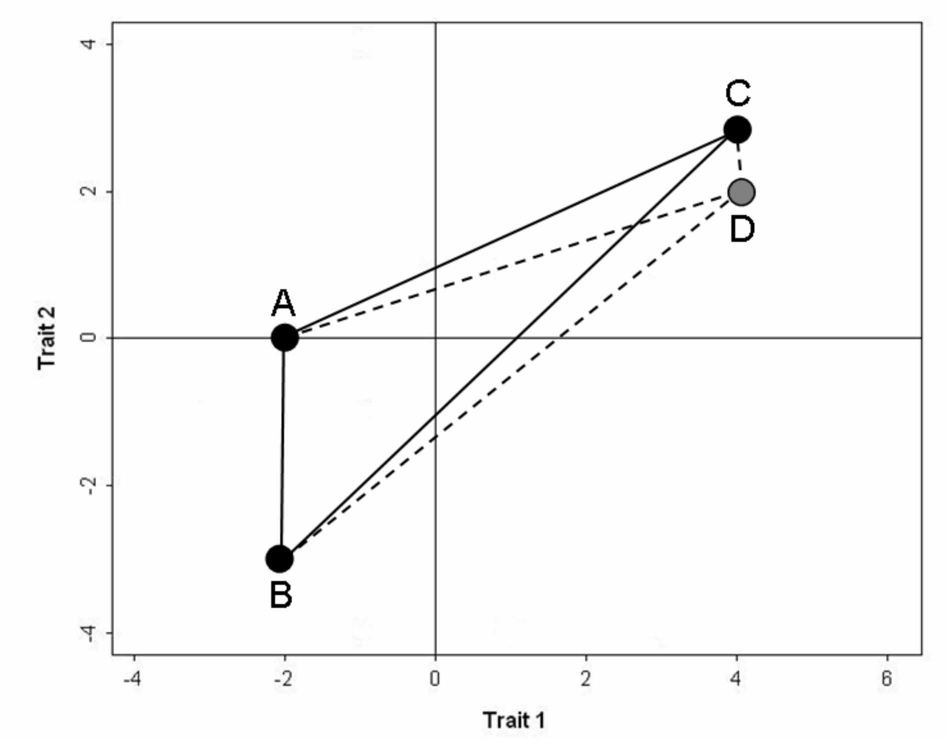

Figure 3.1. Représentation graphique du FAD de Walker *et al.* (1999). L'indice est calculé comme la somme des distances entre toutes les paires d'espèces dans l'espace euclidien défini par les traits considérés. Pour la communauté avec les trois espèces (A, B, C), le FAD est égal à la somme des longueurs des segments continus. Avec une espèce supplémentaire (D), très proche fonctionnellement d'une espèce déjà présente (C), le FAD devient la somme des longueurs des segments continus et tiretés, soit environ deux fois la somme des longueurs des segments continus. Cet exemple illustre le fait que cet indice augmente systématiquement avec le nombre d'espèces ce qui n'est pas souhaitable pour un indice de diversité fonctionnelle.

Suivirent notamment le FD de Petchey & Gaston (2002), le FDvar de Mason *et al.* (2003), le FRO de Mouillot *et al.* (2005a) ou le Q de Botta-Dukat (2005). Ces indices sont valables soit pour un seul trait (FDvar, FRO) soit pour plusieurs (FAD, FD, Q). Néanmoins, aucun ne satisfait aux critères théoriques et pratiques proposés par Mason *et al.* (2003). Par exemple, le FAD est sensible à l'ajout d'une espèce identique à une espèce déjà présente (Figure 3.1) ce qui n'est pas souhaitable. Par ailleurs, certains indices ne prennent pas en compte l'abondance (FD), ce qui est en contradiction avec l'hypothèse du ratio de biomasse de Grime (1998). Par conséquent, aucun indice ne fit consensus ou pris le pas sur les autres (Petchey & Gaston 2006).

En 2005, Mason *et al.* proposèrent un nouveau cadre conceptuel en postulant que la diversité fonctionnelle d'une communauté était la distribution des valeurs de traits et des abondances associées. Ceci n'est donc pas quantifiable via un seul indice et ils proposèrent de considérer trois facettes indépendantes (Figure 3.2).

La première facette est la richesse. Elle correspond à l'espace fonctionnel rempli par la communauté. Elle peut être estimée par l'étendue de la gamme des valeurs présentes et ne prend donc pas en compte les abondances. Plus les valeurs de traits couvrent une grande gamme, plus la richesse est forte. La seconde composante est la régularité, au sens de la régularité dans la distribution des valeurs de traits et de leurs abondances respectives. La régularité est maximale lorsque les espèces ont des valeurs de traits régulièrement espacées et qu'elles ont toutes la même abondance. Cette composante peut être estimée grâce au FRO de Mouillot *et al.* (2005a). Enfin, la troisième composante est la divergence et caractérise la façon dont les abondances sont distribuées par rapport à la valeur moyenne des traits. Elle est maximale lorsque la majorité de l'abondance tend à être associée aux espèces ayant les valeurs de trait extrêmes. Elle peut être quantifiée par le FDvar de Mason *et al.* (2003).

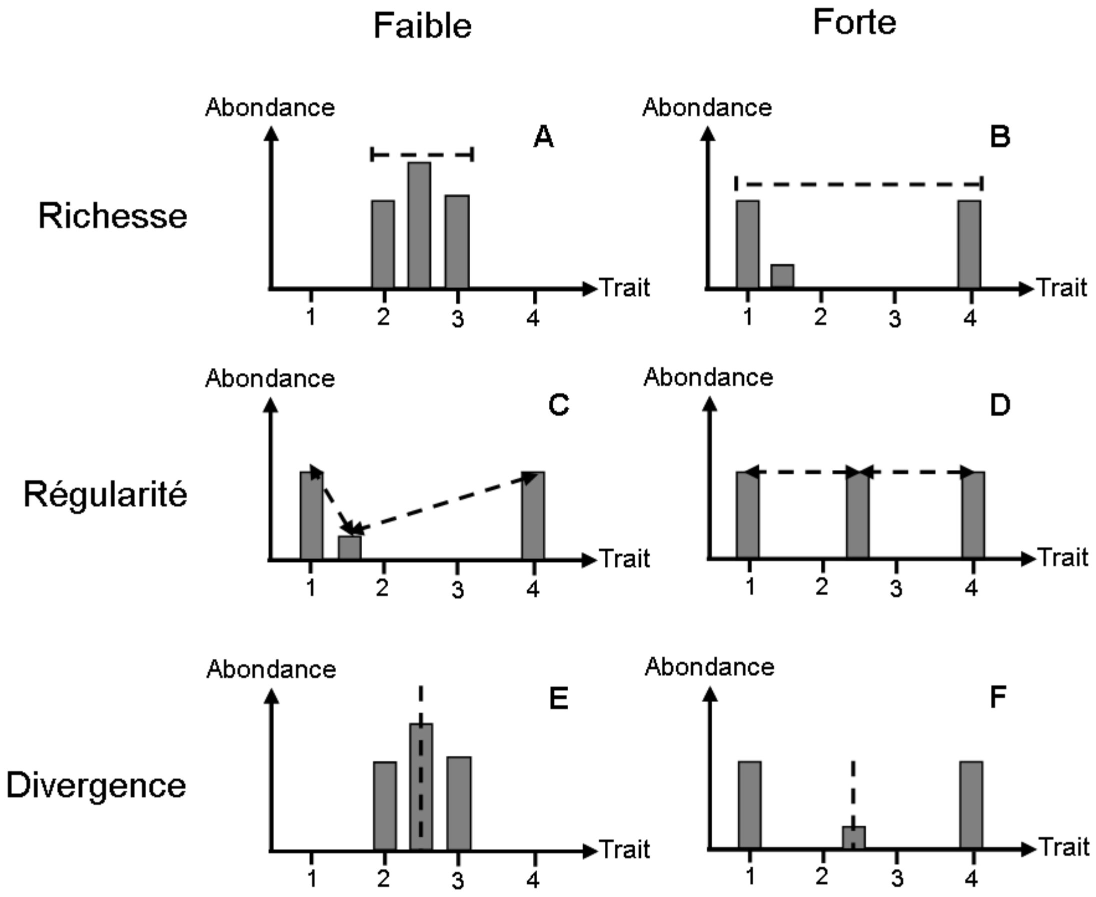

Figure 3.2. Représentation schématique des trois composantes de la diversité fonctionnelle lorsqu’un seul trait est considéré. Pour chaque diagramme, les valeurs de traits pour trois espèces sont représentées en abscisse et leurs abondances respectives sont en ordonnées. Pour chacune des trois composantes, deux exemples contrastés sont présentés. La richesse fonctionnelle correspond à l’étendue des traits présents. La régularité fonctionnelle décrit la régularité de la distribution des espèces dans cette gamme ainsi que celle de leurs abondances. La divergence fonctionnelle représente la distribution des abondances par rapport à la valeur de trait moyenne (illustrée par le tireté vertical).

Il faut souligner que, si ce cadre conceptuel propose une nouvelle façon d’appréhender la diversité fonctionnelle, les indices proposés ne sont valables que pour un seul trait. Or comme cela a été souligné au chapitre précédent, il est très rare de réussir à décrire une fonction biologique avec un seul trait. Par conséquent, nous avons étendu cette approche au cadre général où plusieurs traits sont utilisés (Manuscrit B, Villéger *et al.* 2008). Il est alors possible de définir un espace fonctionnel multidimensionnel où chaque axe représente un trait. Chaque espèce y est positionnée suivant ses valeurs de traits. La diversité fonctionnelle devient donc la répartition des espèces et de leurs abondances dans cet espace multidimensionnel (Figure 1.3).

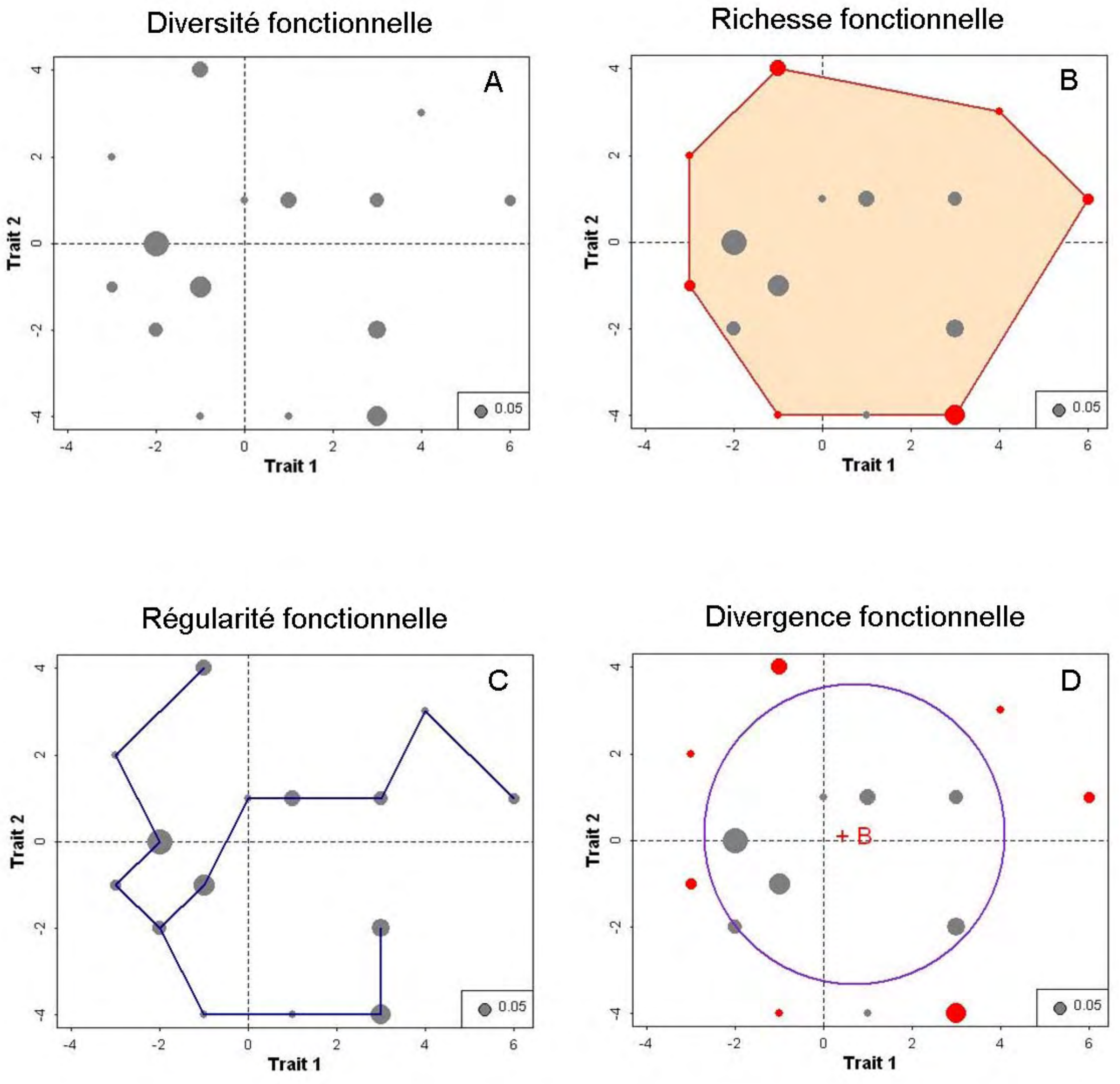

Figure 3.3. Représentation schématique des composantes de la diversité fonctionnelle lorsque plusieurs traits sont considérés. Les quatre diagrammes représentent la même communauté hypothétique de 15 espèces caractérisées pour deux traits fonctionnels (trait 1 et trait 2). Chaque espèce est illustrée par un point dont la position dépend de ses valeurs de traits et dont la surface est proportionnelle à son abondance. La diversité fonctionnelle correspond à la distribution des espèces et de leurs abondances dans l'espace fonctionnel (A). Les trois composantes pour la décrire sont illustrées dans les diagrammes B, C et D (voir texte pour les détails).

La richesse fonctionnelle est influencée par les espèces ayant les valeurs de traits les plus extrêmes (en rouge) qui définissent le volume occupé par la communauté (Figure 3.3B). Elle peut donc être estimée par le volume à l'intérieur de l'enveloppe convexe (en orange), comme proposé par Cornwell *et al.* (2006). La régularité fonctionnelle peut être vue comme la régularité dans la répartition des espèces et de leurs abondances dans ce volume fonctionnel (Figure 3.3C). Elle peut être quantifiée de manière similaire au calcul du FRO (Mouillot *et al.* 2005a) sur l'arbre le plus court reliant tous les points (en bleu). Enfin, la divergence correspond à la répartition des abondances dans le volume fonctionnel (Figure 3.3D). Elle peut être estimée en considérant le centre du volume fonctionnel (point B, centre de gravité des points en rouge), les distances des espèces à ce centre et finalement la déviation à la moyenne de ces distances (cercle violet).

Il est important de noter que ces trois indices sont a priori indépendants et vérifient à eux trois les critères théoriques et pratiques proposés notamment par Mason *et al.* (2003) et Ricotta (2005). Nous avons aussi proposé un cadre d'application général de ces indices dans la perspective d'étudier d'une part la réponse de ces composantes de la diversité fonctionnelle aux conditions environnementales et d'autre part l'effet de ces composantes sur les processus écosystémiques. Nous avons enfin souligné la flexibilité de cette approche, puisque la méthode pour mesurer ces indices reste opérationnelle même lorsque tous les traits ne sont pas quantitatifs et continus. En effet, il est souvent utile de considérer des catégories (par exemple la forme des dents pour les poissons) ou des variables circulaires (par exemple la période de reproduction dans l'année).

Ces trois indices de diversité fonctionnelle ont été mis en pratique sur les communautés de poissons de la lagune de Terminos pour tester l'effet des changements environnementaux sur les facettes de la diversité fonctionnelle (Chapitre 6).

Cette approche de la diversité fonctionnelle dans un espace multidimensionnel présente toutefois une limite pratique. En effet, il est nécessaire d'avoir un nombre d'espèces plus grand que le nombre de traits pour définir l'enveloppe convexe. Par conséquent, pour les communautés pauvres en espèces il n'est pas possible de calculer directement les trois composantes de la diversité fonctionnelle avec les indices décrits précédemment. Il existe deux manières pour pallier à ce problème.

La première consiste tout simplement à réduire le nombre de dimensions de l'espace fonctionnel, par exemple via une Analyse en Composantes Principales sur les traits (ACP). Il suffit alors de ne conserver que quelques composantes principales (entre 2 et 4 suivant le cas d'étude). Ces composantes principales sont des combinaisons linéaires des traits et peuvent donc être considérées comme des traits fonctionnels synthétiques. Néanmoins ces nouveaux « traits » ne représentent qu'une partie de l'information de départ.

L'autre méthode consiste en la construction d'un dendrogramme à partir des distances fonctionnelles entre espèces. Cette méthode est classique en écologie fonctionnelle puisqu'elle sert souvent à définir des groupes fonctionnels en « coupant » les branches de l'arbre à un seuil arbitraire. Néanmoins, ici aussi, la réduction d'une information multidimensionnelle entraîne une perte d'information. Or, il existe plusieurs méthodes pour construire un dendrogramme et le résultat peut fortement être influencé par la méthode.

3.3 Quel dendrogramme pour calculer la diversité fonctionnelle ?

Le calcul de l'indice de diversité fonctionnelle nommé FD (Petchey & Gaston 2002) utilise un dendrogramme construit à partir des distances fonctionnelles mesurées entre les espèces suivant leurs valeurs de traits. Cet indice mesure la somme des longueurs des branches reliant les espèces d'une communauté (Figure 3.4). Pour la construction du dendrogramme, Petchey & Gaston (2002) préconisent l'emploi de la distance euclidienne et de la méthode d'agglomération UPGMA (Unweighted Pair Group Method with Arithmetic mean). Ils n'étayent pas concrètement ce choix arbitraire mais soulignent que le calcul du FD peut être effectué avec d'autres distances ou d'autres algorithmes. Récemment, Podani & Schmera (2006) ont remis en cause l'utilisation systématique de la distance euclidienne pour mesurer la dissimilarité entre les espèces. Ce débat méthodologique a surtout mis en évidence la subjectivité dans la sélection de la métrique utilisée pour le calcul des distances fonctionnelles et dans celle de la méthode d'agglomération pour construire le dendrogramme. Ce problème n'est pas propre à l'indice FD mais à toutes les procédures résumant une information multivariée sur un seul axe (ici un arbre). Cette construction induit forcément une perte d'information, liée à la distorsion, mais en retour elle permet de mieux visualiser les différences entre espèces. Ceci est notamment utile lorsqu'il y a peu d'espèces comparativement au nombre de traits.

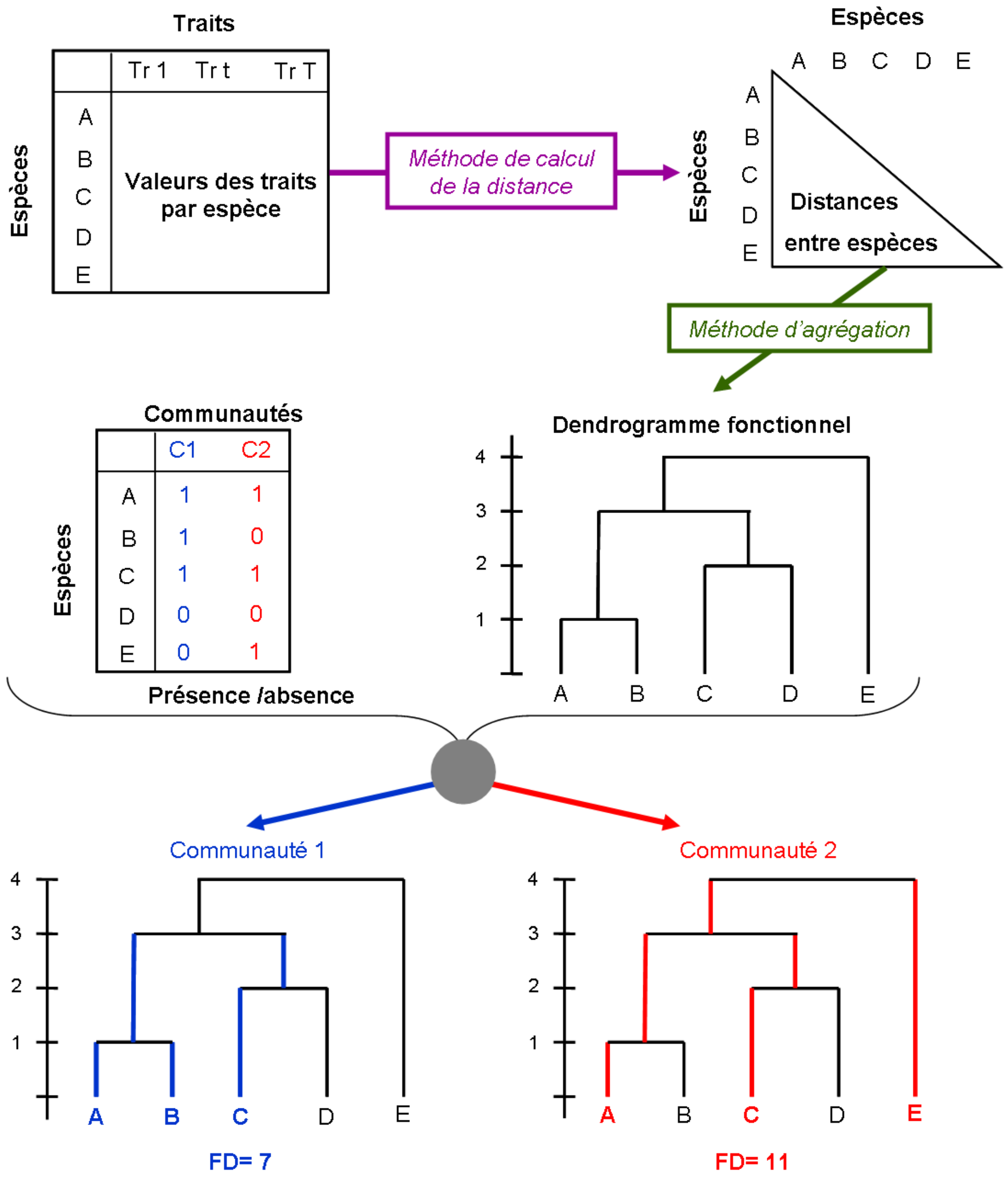

Figure 3.4. Représentation schématique du calcul de l'indice FD. Une matrice de distance est construite à partir des valeurs de traits fonctionnels pour toutes les espèces. Un algorithme d'agrégation est alors utilisé pour construire le dendrogramme. Le FD est finalement calculé comme la longueur des branches de l'arbre reliant les espèces appartenant à la communauté considérée. Les branches horizontales sont juste une convention graphique et n'interviennent pas dans le calcul.

Néanmoins, il apparaît clairement que la diversité fonctionnelle d'une communauté estimée par le FD est directement liée à la topologie de l'arbre. Par conséquent, il est primordial d'établir d'abord un consensus sur la procédure de construction du dendrogramme avant toute interprétation écologique de la diversité fonctionnelle mesurée avec le FD.

En réponse à ce débat, nous avons transposé une méthode initialement développée en phylogénie moléculaire (Manuscrit C, Mouchet *et al.* 2008). Le dendrogramme n'est plus construit avec une méthodologie fixée arbitrairement. Au contraire, tous les dendrogrammes possibles, étant donné le type de distance et la méthode d'agglomération, sont testés et le meilleur d'entre eux est finalement conservé pour calculer le FD. Le critère de sélection retenu est le coefficient de cophénécité. Il mesure la ressemblance entre les distances initiales (calculées sur les valeurs de traits) et les distances mesurées sur l'arbre. Il traduit donc le degré de conservatisme des données brutes à la fin du processus d'agglomération. Grâce à cette méthode objective, le FD est ainsi calculé sans a priori et sur le « moins mauvais » dendrogramme possible, qui plus est en connaissant a posteriori la qualité de ce dernier.

Les simulations menées au cours de notre étude ont notamment mis en évidence qu'aucune méthode n'est systématiquement la meilleure et que bien souvent, le meilleur dendrogramme est obtenu avec un arbre consensus construit avec plusieurs autres arbres. Ce résultat démontre les risques d'erreurs consécutifs à l'emploi du FD tel que proposé initialement par Petchey & Gaston (2002) et soutient la pertinence d'une approche sans a priori.

3.4 Combien la diversité fonctionnelle contient-elle de facettes indépendantes?

Jusqu'ici nous avons fait le postulat que la diversité fonctionnelle ne contient que trois facettes indépendantes. Une question reste donc en suspens : que mesurent les autres indices de diversité fonctionnelle proposés jusqu'alors ? Pour répondre à cette question, nous avons testé le postulat de Mason *et al.* (2005), repris par Villéger *et al.* (2008), suivant lequel la diversité fonctionnelle comprend trois facettes indépendantes (Manuscrit D, Mouchet *et al.* soumis à *Ecology*). Il est intéressant de noter que, suivant les auteurs, différents indices sont proclamés indices de diversité au sens large, de richesse ou de divergence. Ceci est particulièrement flagrant avec l'entropie quadratique (Rao 1982, Botta Dukat 2005) qui à l'origine était présentée comme un indice de diversité fonctionnelle et continue de l'être par certains auteurs (Lepš *et al.* 2006, Weigelt *et al.* 2008). Néanmoins, il est parfois utilisé comme une transposition du FDvar de Mason *et al.* (2005) pour mesurer la divergence en tenant compte de plusieurs traits (Díaz *et al.* 2007, Lavorel *et al.* 2008). Enfin, cet indice est aussi parfois considéré comme un indice de richesse puisqu'il tient compte des distances entres les espèces (Scherer-Lorenzen *et al.* 2008).

De manière plus générale, nous avons sélectionné les huit indices de diversité fonctionnelle les plus utilisés, en l'occurrence les trois indices (FRic, FEve et FDiv) suggérés dans Villéger *et al.* (2008) pris comme référence, le FD dans sa version initiale et dans sa version modifiée (GFD, Mouchet *et al.* 2008), le FAD (Walker *et al.* 1999) et sa version modifiée (MFAD, Schmera *et al.* 2008) et enfin l'entropie quadratique (Q). Ces indices ont été appliqués sur des communautés simulées caractérisées par plusieurs traits. Les résultats montrent que la diversité fonctionnelle comprend bien trois composantes indépendantes. La richesse est décrite par le FRic, le FD, le FAD et leurs versions corrigées (GFD et MFAD). Ceci est logique puisque ces indices ne tiennent compte que de la position des espèces dans l'espace fonctionnel sans considérer les abondances associées. La régularité et la divergence ne sont bien décrites que par les indices ad hoc proposés par Villéger *et al.* (2008). Par contre, il apparaît que l'entropie quadratique est majoritairement liée aux indices de richesse et dans une moindre mesure à la divergence. C'est donc un indice composite, tel l'indice de Shannon qui intègre la richesse et la régularité taxinomique.

Cette étude confirme donc le caractère complexe de la notion de diversité fonctionnelle et l'intérêt d'en considérer les trois facettes grâce à l'utilisation d'indices a priori indépendants. Les indices tels le FD ou l'entropie quadratique ne sont pas a priori les plus pertinents pour cet objectif. Néanmoins, ils présentent des avantages pratiques dans certains cas. Tout d'abord, les indices de Villéger *et al.* (2008) requièrent que le nombre d'espèces soit supérieur au nombre de traits, ce qui n'est parfois pas le cas pour les assemblages pauvres. La richesse fonctionnelle peut alors être estimée par le FD modifié par Mouchet *et al.* (2008). Si par ailleurs les abondances sont connues, l'entropie quadratique permet de mesurer la diversité fonctionnelle de manière synthétique.

3.5 La diversité fonctionnelle inter communautés et la notion de « turnover » fonctionnel

Outre la décomposition de la diversité d'une communauté en facettes complémentaires, il est aussi intéressant de partitionner la diversité à différentes échelles d'observation. La plus couramment utilisée est l'échelle spatiale. Il s'agit alors de comparer la diversité mesurée à l'échelle locale (*i.e.* communautés) avec celle mesurée à l'échelle régionale. Ce partitionnement de la diversité est une thématique ancienne en écologie. Elle s'est développée suite aux travaux fondateurs de Whittaker (1960) qui avait proposé de décomposer la diversité régionale, appelée diversité γ, en une composante locale, appelée α, et une composante appelée β, définie comme la dissimilarité entre les deux niveaux de diversité ou comme le « turnover » entre les communautés locales.

Les premiers travaux utilisant ce cadre conceptuel utilisaient une décomposition multiplicative où : $\gamma = \alpha \times \beta$. Néanmoins, Lande (1996) suggéra d'adopter plutôt une décomposition additive afin d'avoir l'homogénéité des unités : $\gamma = \alpha + \beta$. De nombreux indices pour quantifier le degré de turnover ou dissimilarité (β) ont été proposés (voir la revue de Koleff *et al.* 2003). La très grande majorité n'est valable que sur le cas le plus simple, c'est-à-dire lorsqu'il n'y a que deux communautés. Par ailleurs, la notion de diversité β est utilisée en considérant seulement la diversité taxinomique, sans tenir compte de l'identité biologique des espèces.

Or, il est primordial d'aller plus loin que la simple composition en espèces. En effet, si celle-ci est très utile en première approximation, elle ne permet pas de décrire la biologie des espèces, ni leur dominance dans les communautés. Prenons trois cas hypothétiques (Figure 3.5), ayant chacun deux communautés ne partageant aucune espèce. Par conséquent, la diversité β taxinomique est forte dans les trois cas. Cependant, alors que dans le cas 1 les communautés possèdent des espèces très différentes morphologiquement, dans les cas 2 et 3, les espèces sont très similaires entre les communautés. Néanmoins, dans le cas 2, les espèces respectivement dominantes ne se ressemblent pas fonctionnellement. Intuitivement, il apparaît donc que la diversité β fonctionnelle est forte dans les cas 1 et 2 alors qu'elle est faible dans le cas 3.

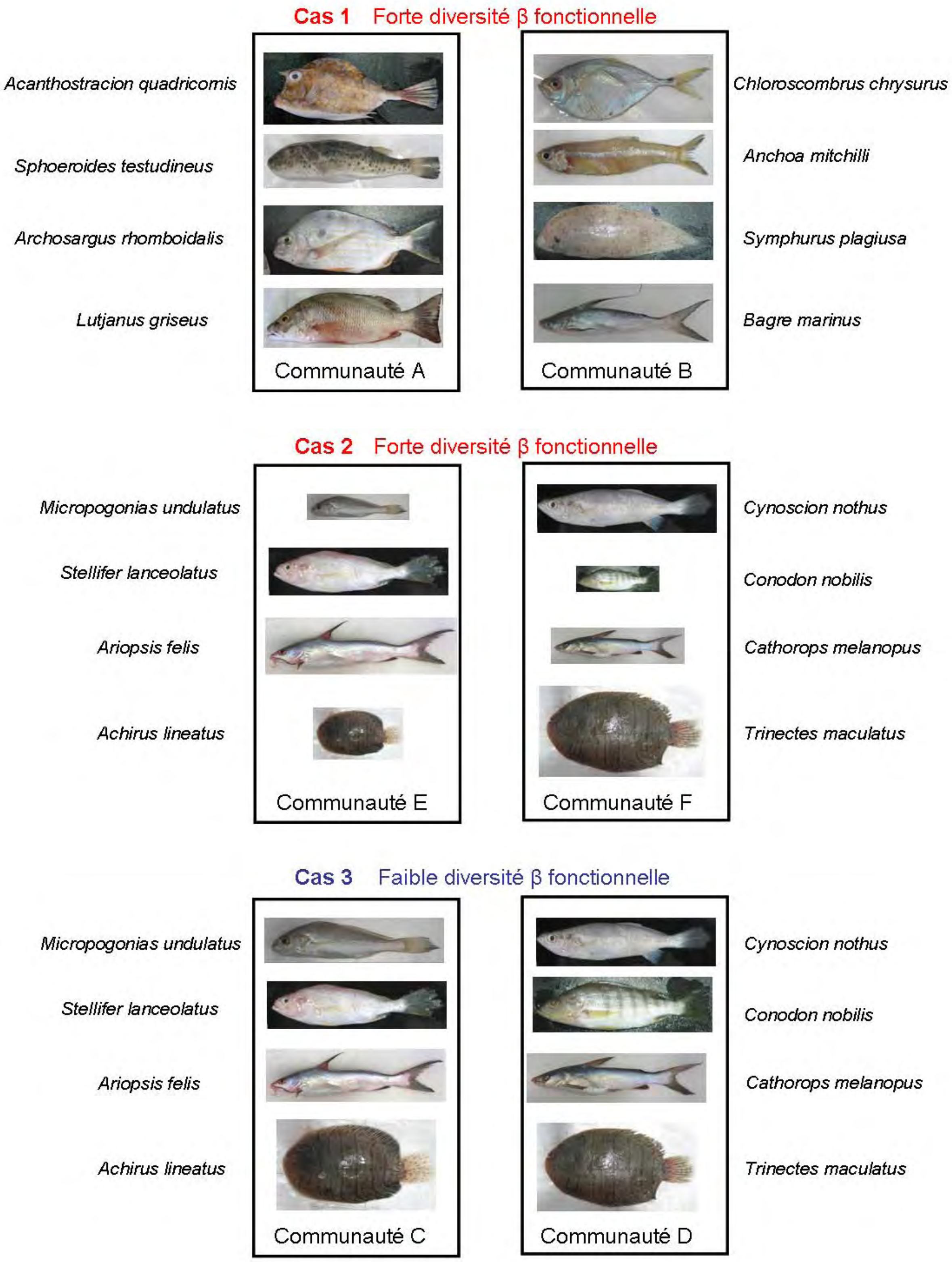

Figure 3.5. Illustration de la notion de diversité β fonctionnelle. Dans le cas 2, la taille des photos est proportionnelle à l'abondance de l'espèce. Dans les trois cas, la diversité β taxinomique est maximale (aucune espèce en commun entre les deux communautés).

Nous avons donc développé une décomposition de la diversité fonctionnelle en composantes γ, α et β (Manuscrit E, Villéger & Mouillot 2008). Pour cela, nous avons en fait repris et corrigé la décomposition de la diversité phylogénétique proposée par Hardy & Senterre (2007). Cette décomposition, déjà évoquée par Ricotta (2005), repose sur l'utilisation de l'indice d'entropie quadratique de Rao (1982). Cet indice de diversité présente l'avantage d'être synthétique et de considérer à la fois les différences entre espèces, quelles soient fonctionnelles ou phylogénétiques, et leurs abondances relatives.

Dans cet article nous avons notamment corrigé la formule de Hardy & Senterre (2007) dédiée au calcul de la moyenne des diversités locales (α). En effet, leur mode de calcul ne tenait pas compte des contributions des communautés locales à l'abondance totale. Cette erreur conduisait dans certains cas à des valeurs de diversité β négatives, ce qui est théoriquement impossible.

De plus, outre cette correction, nous avons démontré que la diversité fonctionnelle β tendait vers 0 lorsque les espèces, ou les groupes d'espèces fonctionnellement proches, avaient toujours la même abondance dans les communautés locales (cas 3 de la Figure 3.5). Au contraire, la diversité β augmente lorsque les communautés locales tendent à avoir des structures fonctionnelles différentes, autrement dit lorsque leurs espèces dominantes respectives sont fonctionnellement très différentes.

Cette décomposition de la diversité fonctionnelle à plusieurs échelles a été mise en œuvre pour étudier la stabilité spatio-temporelle de la structure fonctionnelle des communautés de poissons de la lagune de Terminos (Chapitre 5).

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NEW MULTIDIMENSIONAL FUNCTIONAL DIVERSITY INDICES FOR A MULTIFACETED FRAMEWORK IN FUNCTIONAL ECOLOGY

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Abstract. Functional diversity is increasingly identified as an important driver of ecosystem functioning. Various indices have been proposed to measure the functional diversity of a community, but there is still no consensus on which are most suitable. Indeed, none of the existing indices meets all the criteria required for general use. The main criteria are that they must be designed to deal with several traits, take into account abundances, and measure all the facets of functional diversity. Here we propose three indices to quantify each facet of functional diversity for a community with species distributed in a multidimensional functional space: functional richness (volume of the functional space occupied by the community), functional evenness (regularity of the distribution of abundance in this volume), and functional divergence (divergence in the distribution of abundance in this volume). Functional richness is estimated using the existing convex hull volume index. The new functional evenness index is based on the minimum spanning tree which links all the species in the multidimensional functional space. Then this new index quantifies the regularity with which species abundances are distributed along the spanning tree. Functional divergence is measured using a novel index which quantifies how species diverge in their distances (weighted by their abundance) from the center of gravity in the functional space. We show that none of the indices meets all the criteria required for a functional diversity index, but instead we show that the set of three complementary indices meets these criteria. Through simulations of artificial data sets, we demonstrate that functional divergence and functional evenness are independent of species richness and that the three functional diversity indices are independent of each other. Overall, our study suggests that decomposition of functional diversity into its three primary components provides a meaningful framework for its quantification and for the classification of existing functional diversity indices. This decomposition has the potential to shed light on the role of biodiversity on ecosystem functioning and on the influence of biotic and abiotic filters on the structure of species communities. Finally, we propose a general framework for applying these three functional diversity indices.

Key words: competitive filtering; environmental filtering; functional divergence; functional evenness; functional niche; functional richness; functional traits; null model.

INTRODUCTION

The functional diversity of a community has emerged as a facet of biodiversity quantifying the value and range of organismal traits that influence their performance and thus ecosystem functioning (Diaz and Cabido 2001). There is an increasing body of literature demonstrating that functional diversity, rather than species diversity, enhances ecosystem functions such as productivity (Tilman et al. 1997, Hooper and Dukes 2004, Petchey et al. 2004, Hooper et al. 2005), resilience to perturbations or invasion (Dukes 2001, Bellwood et al. 2004), and regulation in the flux of matter (Waldbusser et al. 2004). However, most of this work has used functional-group richness as a surrogate for functional diversity. Gathering species into groups results in the loss of information and the imposition of a discrete structure on functional differences between species, which are usually continuous (Gitay and Noble 1997, Fonseca and Ganade 2001). Further, most studies using functional groups ignore species abundances, and some species may have a much greater impact on ecosystem functioning because of their greater abundance (Diaz and Cabido 2001). Finally, a functional-group approach may produce different conclusions on the importance of functional diversity for ecosystem functioning depending on the classification method employed (Wright et al. 2006). Thus, there is an urgent need to provide continuous measures of functional diversity that directly use quantitative values for functional traits.

Since 1999, many indices of functional diversity have been published (reviewed in Petchey and Gaston 2006). These indices include a priori classifications (number of functional groups), the sum (FAD; Walker et al. 1999) or

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average (quadratic entropy; Botta-Dukat 2005) of functional distances between species pairs in multivariate functional trait space, distances between species along hierarchical classifications (FD; Petchey and Gaston 2002), and the distribution of abundance along functional trait axes (FDvar; Mason et al. 2003). However, despite the number and variety of these indices, no consensus has arisen on the sensitive question of how to measure functional diversity (Petchey and Gaston 2006). Existing indices have four main limitations:

1) None but FDvar (Mason et al. 2003), the functional regularity index (FRO) of Mouillot et al. (2005), and quadratic entropy (Botta-Dukát 2005) take into account the relative abundance of species. However, as suggested by Grime (1998), the effect of each species has to be weighted according to its abundance in order to reflect its contribution to ecosystem functioning.

2) Some indices are only designed for single-trait approaches (Mason et al. 2005) and as such may give an incomplete image of functional diversity when many traits are used to characterize species functional niches.

3) Some indices are trivially related to species richness, especially the FAD of Walker et al. (1999), where the addition of a new species that is completely identical functionally to another one already in the community causes an augmentation of functional diversity.

4) While indices based on sum of lengths on hierarchical classifications do not take account of abundances, they may deal with many traits simultaneously and are not trivially related to species richness (e.g., the FD index of Petchey and Gaston 2002). Nevertheless, building a classification from the matrix of distances between species pairs leads to a loss of information and modifies the initial interspecific functional distances (as demonstrated by Podani and Schmera [2006]). In other words, a species classification cannot match exactly the relative position of species in a multidimensional functional trait space, and the arbitrary choices in the way of constructing classifications may drastically influence the functional diversity estimation (Podani and Schmera [2007]; but see Petchey and Gaston [2007]).

Recently, Mason et al. (2005) argued that functional diversity cannot be summarized by a single number. Instead they proposed a framework where functional diversity is composed of three independent components—functional richness, functional evenness, and functional divergence—which need to be quantified separately. The interest of splitting functional diversity into three independent components is to provide more detail in examining the mechanisms linking biodiversity to ecosystem functioning. For example, Mason et al. (2008) demonstrated how the primary functional diversity components could be used in combination to test competing hypotheses for species–energy relationships. Moreover, the search for the effects of biotic interactions and environmental filters on biodiversity patterns may benefit from the proposition of such independent "facets" of functional diversity, since variation in the volume of functional-trait space filled by species does not have the same meaning as a shift in the distribution of abundance within that space. The former may indicate an increasing pressure of environmental filters (Cornwell et al. 2006), while the latter may reveal a shift in the intensity of competitive interactions (Mason et al. 2007, 2008).

However, the indices proposed by Mason et al. (2005) are estimated based on single traits and are not directly transposable for multiple-trait approaches. Here we aim to estimate the three primary components of functional diversity using one existing and two novel indices that are specifically designed to incorporate multiple functional traits. These indices directly measure the distribution of species in multivariate functional trait space and are independent of species richness and each other. We present these indices as general tools for quantifying the functional diversity of any community and propose a practical framework for their application. This framework is based on the use of null models to allow comparison of communities from different species pools and with different species richness. It is hoped this framework will aid in exploring biodiversity–environment–ecosystem functioning relationships in ecology, as well as elucidating processes of community assembly (e.g., Mason et al. 2008).

MULTIDIMENSIONAL FUNCTIONAL DIVERSITY INDICES

As proposed by Keddy (1992), functional ecologists generally have, for their communities of interest, a matrix with values for selected functional traits for each species. From a geometrical point of view, a species' functional niche may be described by its position in a functional-trait space (Rosenfeld 2002). Assuming that we have T functional-trait values for each species of a given community, the functional-niche space is then the T dimensional space defined by the T axes, each one corresponding to a trait.

We suggest standardizing trait values (mean of 0 and unit variance) so that each trait has the same weight in functional diversity estimation and the units used to measure traits have no influence. The community studied is composed of S species. Any species i has T traits of standardized values ($x_{i1}, x_{i2}, \ldots, x_{iT}$) which are conceived as coordinates in the functional trait space.

When plotting all the S species in a multi-trait space, functional diversity is simply the distribution of species and their abundances in this functional space (Fig. 1a, circles represent species, and diameters are species relative abundances). The indices presented here aim at describing how much space is filled and how the abundance of a community is distributed within this functional space. In the following paragraphs we will keep this general framework of S species plotted in a T dimensional space.

Relative abundances of species are noted ($w_1, w_2, \ldots w_S$), with $\Sigma_{i=1}^{S} w_i = 1$.

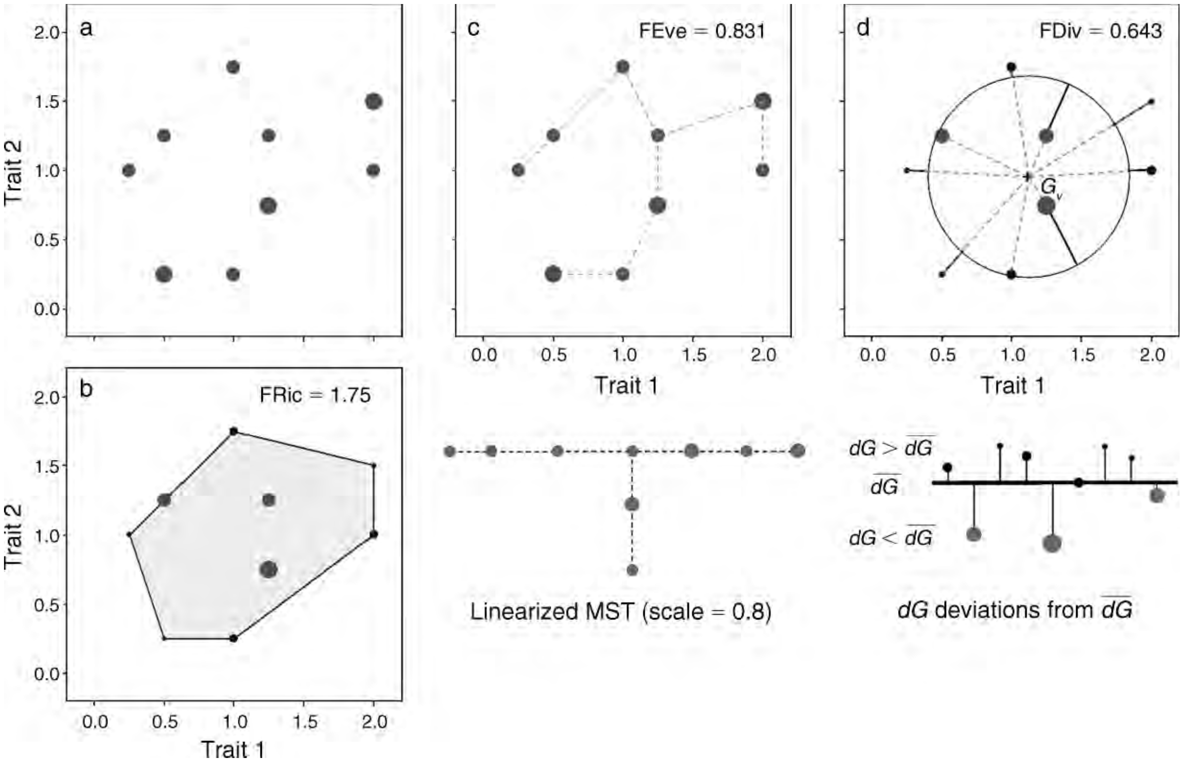

FIG. 1. Estimation of the three functional diversity indices in multidimensional functional space. For simplification, only two traits and nine species are considered. (a) The points are plotted in the space according to the trait values of the corresponding species. Circle diameters are proportional to species abundances. In (b), the convex hull is drawn with a solid black line; the points corresponding to the vertices are black, and the convex hull volume is shaded in gray. The functional richness (FRic) corresponds to this volume. (c) The minimum spanning tree (MST, dashed line) links the points. Functional evenness (FEve) measures the regularity of points along this tree and the regularity in their abundances. For convenience, the tree is plotted stretched under the panel. (d) The position of the center of gravity of the vertices ("G_V," black cross), the distances between it and the points representing the species (gray dashed lines), and the mean distance to the center of gravity (large circle with the black line border). The deviation of the distances from the mean corresponds to the length of the black line linking each point and the large circle with the black line border. This distribution is also represented under the panel. The more the high abundances are greater than the mean, the higher the functional divergence (FDiv).

Following Grime (1998), who underlined the biomass ratio effect, we suggest that good sets of functional diversity indices have to take into account biomass, or at least another estimation of abundance (e.g., number of individuals, percent cover, or density). Indeed, biomass is directly linked to the amount of energy and resources assimilated within a species. Hence, we prefer this measure of abundance even if the indices may incorporate any measure of abundance, since they are based on relative abundances, which are by definition unitless. All of our indices are also suitable for presence/absence data, which is actually a particular case where each species has a relative abundance of $1/S$. We will give a brief description of each primary functional diversity component and outline the indices we propose for their measurement in multivariate functional trait space.

Functional richness

Functional richness represents the amount of functional space filled by the community. For a single-trait approach, the functional richness may be estimated as the difference between the maximum and minimum functional values present in the community (Mason et al. 2005). For multiple-trait studies, functional richness is more challenging to measure, as the index has to estimate the volume filled in the T dimensional space by the community of interest. Recently, Cornwell et al. (2006) proposed the convex hull volume as a measure of the functional space occupied by a community. The convex hull is actually the minimum convex hull which includes all the species considered; the convex hull volume is then the volume inside this hull (Fig. 1b).

Thus, if two species a and b are inside the convex hull volume, whose coordinates (i.e., traits values) are respectively $(x_{a1}, x_{a2}, \dots x_{aT})$ and $(x_{b1}, x_{b2}, \dots x_{bT})$, then any hypothetical species with coordinates $(Kx_{a1} + (1 - K)x_{b1}, Kx_{a2} + (1 - K)x_{b2}, \dots, Kx_{aT} + (1 - K)x_{bT})$ for $0 \leq K \leq 1$ is also in the convex hull volume. This measure of space occupancy corresponds to a multivariate range. Any species whose trait values are less extreme for all traits than those of the two existing species will be included inside the convex hull volume.

Basically, the convex hull volume algorithm determines the most extreme points (hereafter named vertices, the black circles on Fig. 1b), links them to build the convex hull (lines on Fig. 1b), and finally calculates the volume inside. Therefore, we propose to use the value of the convex hull volume filled by a community as a multidimensional measure of the functional richness (Cornwell et al. 2006, Layman et al. 2007).

We suggest computing the convex hull volume with the Quickhull algorithm (Barber et al. 1996). The number of species must be higher than the number of traits ($S > T$), and the species must not be distributed in a line (in which case the hull volume is zero). The program returns the volume and the identity of the species forming the vertices.

Functional evenness

Functional evenness describes the evenness of abundance distribution in a functional trait space (Mason et al. 2005). The functional regularity index (FRO) has been proposed for the estimation of functional evenness when using a single trait (Mouillot et al. 2005). This index measures both the regularity of spacing between species along a functional trait gradient and evenness in the distribution of abundance across species. FRO takes a value of 1 when the distances between all nearest neighbor species pairs are identical and when all species have the same abundance. Conversely, FRO will approach 0 when some species are tightly packed along the functional axis, with a high proportion of abundance concentrated within a narrow part of the functional-trait gradient. It has the advantage of being independent from species richness, functional richness, and functional divergence. While an extension to multiple trait studies has been proposed for FRO (Mouillot et al. 2005), this method is dependent on ordination techniques and consequently risks the loss of information, especially for traits that are weakly correlated with other traits.

In order to transform species distribution in a T-dimensional functional space to a distribution on a single axis, we choose to use the minimum spanning tree (noted MST hereafter). The MST is the tree that links all the points contained in a T-dimensional space with the minimum sum of branch lengths (Fig. 1d). We compute the MST thanks to the "ape" R-package, which returns the $S - 1$ branches between the S species. By direct analogy to Mouillot et al. (2005), our new functional evenness index measures both the regularity of branch lengths in the MST and evenness in species abundances. As a first step, for each branch l of the MST (dashed line on Fig. 1d), the length is divided by the sum of the abundances of the two species linked by the branch

$$\mathrm{EW}_l = \frac{\mathrm{dist}(i,j)}{w_i + w_j}$$

where EW is weighted evenness, $\mathrm{dist}(i, j)$ is the Euclidean distance between species i and j, the species involved is branch l, and w_i is the relative abundance of species i.

Then, for each of these branches, the value of EW_l is divided by the sum of EW values for the MST to obtain the partial weighted evenness (PEW), defined as

$$\mathrm{PEW}_l = \frac{\mathrm{EW}_l}{\sum_{l=1}^{S-1} \mathrm{EW}_l}.$$

In the case of perfect regularity of abundance distribution along the MST, all EW_l will be equal and all PEW_l values will be $1/(S - 1)$. Conversely, when PEW_l values differ among branches, the final index must decrease. To this aim we compared PEW_l values to $1/(S - 1)$. Finally, our functional evenness index is

$$\mathrm{FEve} = \frac{\sum_{l=1}^{S-1} \min\left(\mathrm{PEW}_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}.$$

The term $1/(S - 1)$ is subtracted from the numerator and denominator because there is at least one value of PEW_l which is less than or equal to $1/(S - 1)$ whatever S is (see Bulla [1994] for more details about this standardization). Therefore, FEve is not biased by species richness and is constrained between 0 and 1. We obtain 1 when all PEW_l are equal to $1/(S - 1)$. FEve is also independent of the convex hull volume, as it is unitless. We need at least three species to define an MST and then estimate FEve.

Basically, the new index quantifies the regularity with which the functional space is filled by species, weighted by their abundance. FEve decreases either when abundance is less evenly distributed among species or when functional distances among species are less regular (Fig. 2).

Functional divergence

For a single-trait approach, functional divergence represents how abundance is spread along a functional trait axis, within the range occupied by the community (Mason et al. 2005). For instance, divergence is low when the most abundant species have functional traits that are close to the center of the functional trait range. Conversely, when the most abundant species have extreme functional trait values, then divergence is high. In a multivariate context, functional divergence relates to how abundance is distributed within the volume of functional trait space occupied by species (Fig. 1c).

One complication is finding a method to measure functional divergence that is independent of the volume of functional trait space occupied and the evenness of abundance distribution with that volume. Here we present a novel index to achieve this. Firstly, the coordinates of the center of gravity G_V (g_1, g_2, ... g_T) of the V species forming the vertices of the convex hull are calculated as follows:

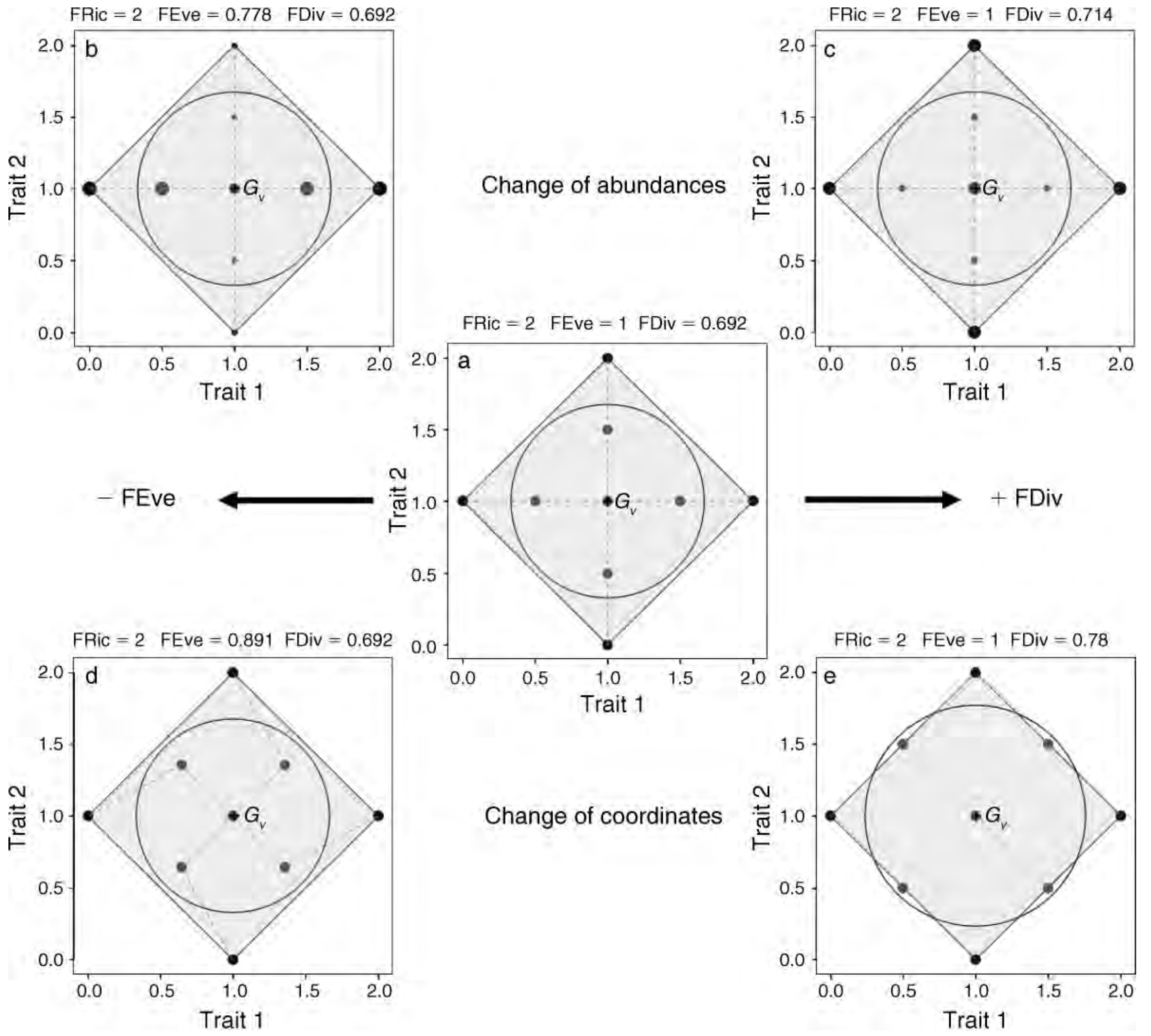

FIG. 2. The center panel (a) is the reference showing that there are nine species and two traits. The figure shows the effect of changes in (d, e) the identities of species and (b, c) their relative abundance on functional divergence (FDiv) and functional evenness (FEve). The key to symbols and lines is the same as for Fig. 1. For simplicity, the coordinates of the extreme points are the same for all the figures, as are functional richness values (FRic) and the shape of the convex hull.

$$g_k = \frac{1}{V}\sum_{i=1}^{V} x_{ik}$$

where x_{ik} is the coordinate of species i on trait k [1, T].

Second, for each of the S species, we calculate the Euclidean distance to this center of gravity:

$$dG_i = \sqrt{\sum_{k=1}^{T}(x_{ik} - g_k)^2}.$$

The mean distance of the S species to the center of gravity ($\overline{dG}$) is then calculated:

$$\overline{dG} = \frac{1}{S}\sum_{i=1}^{S} dG_i.$$

It is important to note that the coordinates of the center of gravity are calculated only on vertices coordinates without taking into account relative abundances; this implies that dG_i and thus $\overline{dG}$ values are only influenced by the shape and the volume of the scatter plot of the S species (Fig. 2).

Then, the sum of abundance-weighted deviances (Δd) and absolute abundance-weighted deviances ($\Delta|d|$) for distances from the center of gravity are calculated across the species:

$$\Delta d = \sum_{i=1}^{S} w_i \times (dG_i - \overline{dG})$$

and

TABLE 1. Summary of the criteria of Mason et al. (2003) and Ricotta (2005) and properties of our three indices (FRic for functional richness, FDiv for functional divergence, and FEve for functional evenness) for these criteria.

Criteria	FRic	FEve	FDiv
Positive values†	yes	yes	yes
Be constrained to a 0–1 range (for convenience) and use that range well‡		yes	yes
Be unaffected by the units in which the abundance is measured†	yes	yes	yes
Reflect the contribution of each species in proportion to its abundance†		yes	yes
Be unaffected by the units in which the character is measured†		yes	yes
Reflect the range of character values present†	yes		
Be unaffected by the number of species†		yes	yes
Be unaffected when a species is split in two species with the same traits values and the same total abundance†	yes		yes
Set monotonicity (a subset of a community is less diverse that this community)‡	yes		
Concavity (a set of communities is in mean less diverse than the aggregated pool)‡	yes		

Note: Empty cells did not meet the criteria of that particular index.
† These criteria are from Ricotta (2005).
‡ These criteria are from Mason et al. (2003).

$$\Delta|d| = \sum_{i=1}^{S} w_i \times |dG_i - \overline{dG}|.$$

Functional divergence may then be calculated as

$$\mathrm{FDiv} = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}.$$

Values of dG_i are Euclidean distances and thus are positive or null, hence Δd is bounded between $\overline{dG}$ and $\Delta|d|$. Therefore, addition of $\overline{dG}$ to the numerator and denominator ensures that the index ranges between 0 and 1. The index approaches 0 when highly abundant species are very close to the center of gravity relative to rare species (Δd is negative and tends to $-\overline{dG}$), and it approaches unity when highly abundant species are very distant from the center of gravity relative to rare species (Δd is positive and tends to $\Delta|d|$; see Fig. 2 for illustration).

For presence/absence data, functional divergence is the highest if all the species are on the convex hull and at equal distance to its center of gravity (i.e., if the center of gravity of the convex hull is also a center of symmetry of the functional space). This condition is actually true whatever the relative abundances of species.

Given that the distances considered in the formula are those from the center of gravity of the vertices, functional divergence is a priori independent from the shape and the volume of the convex hull and so from the functional richness index. A script (R statistical language [R development Core Team 2007]) to compute the three indices is *available online*.[4]

ASSESSING THE VALIDITY OF THE INDICES

Some authors have proposed criteria that functional diversity indices have to match (Mason et al. 2003, Ricotta et al. 2005, Petchey and Gaston 2006). From these published criteria we selected 10 that appear relevant for a multidimensional approach (and which are not contradictory). We do not expect that each of our three indices matches each criterion but rather that the ensemble of indices does (Table 1).

First, our three indices are positive, and the higher they are, the higher the component of functional diversity they quantify is. Functional divergence (FDiv) and functional evenness (FEve) are strictly constrained between 0 and 1. Functional richness has no upper limit because it quantifies an absolute volume filled, which depends partly on the number of traits and on their unit. However, functional richness values may be constrained between 0 and 1 via standardization by the global hull volume (e.g., the volume occupied by all species considered in a particular study, as proposed for the FR_i index of Mason et al. 2005). The three indices are independent of the unit used to measure species abundances. Indeed, functional richness is, by construction, independent of species abundances while functional divergence and functional evenness take into account species relative abundances, which are unitless. Functional divergence and functional evenness both reflect the distribution of species abundances in functional space, and thus the contribution of each species to functional divergence and functional evenness is proportional to its abundance.

Functional richness is the only index that reflects the range of the trait values and thus, as expected, is affected by the unit of the traits (Fig. 3). However, as noted previously, this may be accounted through standardization by the maximum possible hull volume. The three indices are not affected by a translation or a rotation of the functional space of reference (Fig. 3).

To test whether our indices match the criteria of independence with species richness and whether our indices are independent from each other, we generated artificial communities. The number of traits was fixed to three. Coordinates of the species for each axis were generated using a uniform distribution (i.e., all values had equal chance of being selected) within a range of 10. Seven species richness values were considered (10, 15, 20, 25, 30, 35, and 40). Species abundances were generated

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[4] ⟨http://www.ecolag.univ-montp2.fr/software/⟩

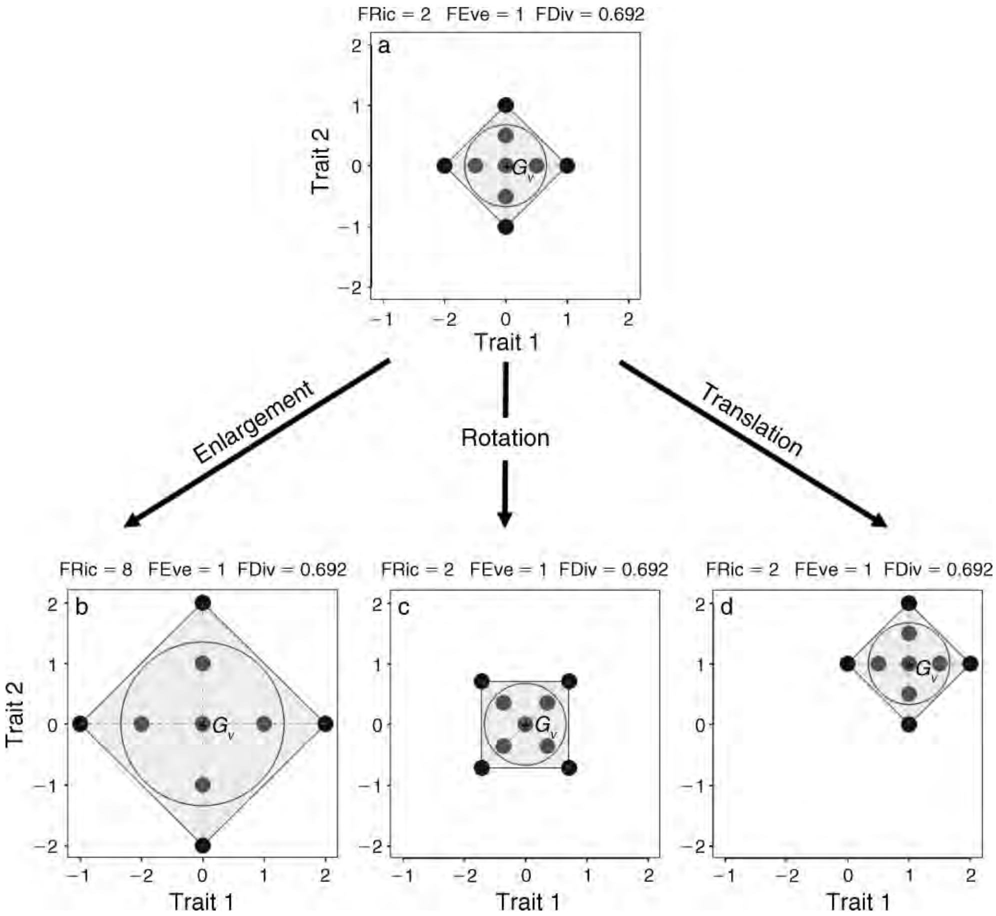

FIG. 3. Properties of the three functional diversity indices (FRic for functional richness, FDiv for functional divergence, and FEve for functional evenness). Two traits (axes) and nine species (points) with equal abundances are considered for graphical commodity. The key to the symbols and lines is the same as for Fig. 1. Panel (a) is the community of reference. Two communities with (c) a rotation or with (d) a translation between them have similar functional richness, functional evenness, and functional divergence. However, (b) two communities having the same shape but different sizes have similar functional evenness and functional divergence while having different functional richness values.

using a uniform distribution within a range of 100 and then standardized to relative abundances. One hundred replicates (coordinates and abundances) were generated using R software for each of these seven cases. The three indices were computed for these 700 data sets. Pearson's coefficients of correlation between each index and species richness and between the three indices were then tested.

Our simulations using artificial data sets showed clearly that functional richness and species richness are strongly and positively related ($r = 0.872$, $P < 0.001$; Fig. 4a). As expected from the sampling effect, it is more likely to obtain a larger hull volume with more species in the community. However, for a given T-dimensional functional space, the maximal convex hull is obtained with 2^T species whose coordinates are a combination of the extreme values on each axis. In other words, in such a given Euclidian space, the maximal volume given the ranges on the axes is a hypervolume with all its angles square. For example, with a three-dimensional space, the maximum convex hull volume is obtained with at least eight points constituting a cube. It is impossible to fill the whole available space with fewer than eight species. This property means that for communities with species richness less than 2^T, observed functional richness values are not comparable. Practically, to avoid this bias, the number of species must increase exponentially with the number of traits in comparative studies. Cornwell et al. (2006) do not explicitly point out this bias in their study, but they overcome it using a randomization procedure allowing the observed functional richness value to be compared with that expected at random for the species richness level of the community. This limit partly explains the positive correlation between the convex hull volume index and species richness, the shape of the relation depending on the number of traits, and on their correlations.

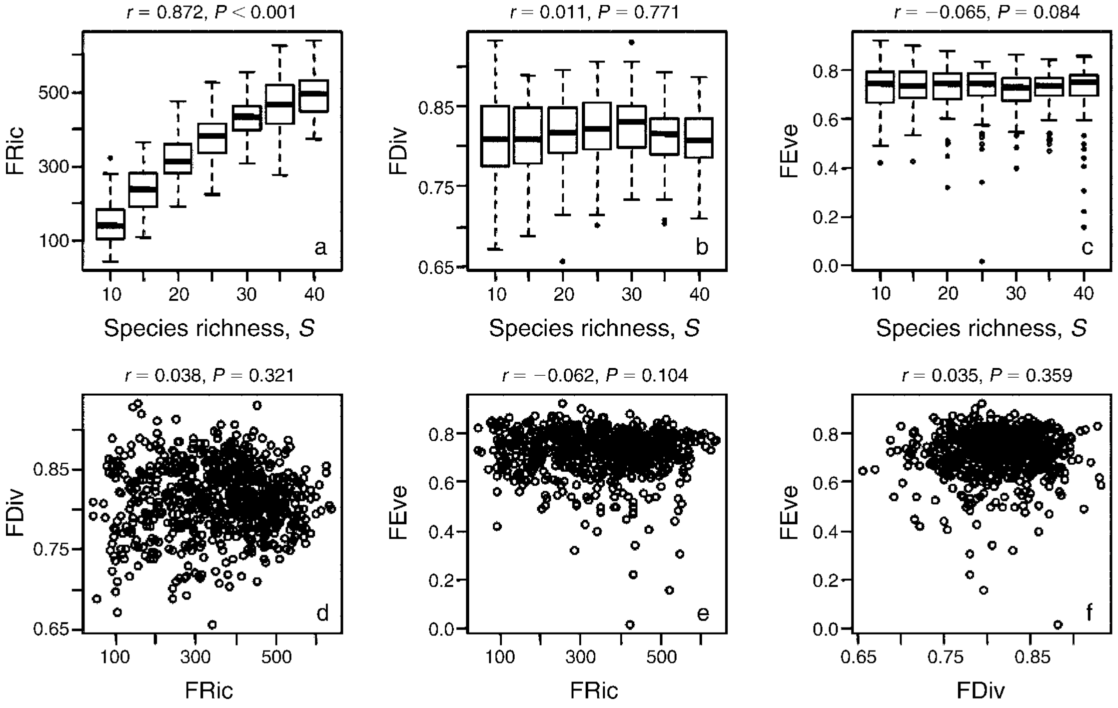

FIG. 4. Properties of the three functional diversity indices for artificial communities. Three traits were considered, and both the coordinates and the abundances of the species were generated under a uniform law (with respective range of 10 and 100). Seven species richness levels (*S*) were considered. Each species richness level was replicated 100 times. For each community, functional richness (FRic), functional divergence (FDiv), and functional evenness (FEve) were estimated. The first three panels (a, b, c) show the relations between each index and species richness. The three last panels (d, e, f) present the correlations between the three indices. Pearson's coefficients of correlation and levels of significance are given above the panels. FRic is the only index correlated to species richness. The three indices are independent of each other.

The values obtained with artificial communities showed that functional divergence and functional evenness are independent from species richness (Fig. 4b, c). These two indices are also independent from functional richness (Fig. 4d, e) and each other (Fig. 4f).

Two of the three indices satisfied the modified twinning criterion proposed by Mason et al. (2003), that diversity is not affected when a species is replaced by two species with the same trait values and the same total abundance. If the species is a vertex, the convex hull volume algorithm will consider only one of the two twins as a vertex and thus the convex hull, and so the richness will not be modified. Similarly, the position of the center of gravity of the vertices will not be affected. Moreover, the Δd and $\Delta|d|$ of the FDiv computation will be unchanged by the fact that the abundance is split between two entities having the same position. On the contrary, the evenness index does not satisfy this criterion. If a species is split into two species identical for all traits and which share the initial abundance, the regularity of trait values will be changed, as there are now two species at the same place in the functional space. It is not a bias of our index but is inherent to our definition of functional evenness. This would only be problematic when it is difficult to identify species with certainty or where taxonomic opinion differs as to whether a subspecific taxon should be treated as a separate species. Thus, we believe that the latter point, indices independent from species richness, is far more important in the ecological context.

Functional richness is the only index in accordance with the monotonicity criterion proposed by Ricotta et al. (2005). Indeed, the functional-richness value of a subset of species cannot be superior to the functional-richness value of the whole set. Functional divergence and functional evenness do not match this criterion, as the addition of species can decrease functional divergence (a new abundant species close to the center of gravity of the functional space) and functional evenness (a new species close to an abundant species), because these indices consider relative abundances.

Similarly, functional richness is the only index to respect the concavity criterion, for the same reason as for the monotonicity criterion. By contrast, indices of divergence and evenness are not additive, which means that the divergence (or the evenness) of two communities is not linked to the mean of the two index values but depends on the characteristics of the new constructed community (species traits and relative abundances).

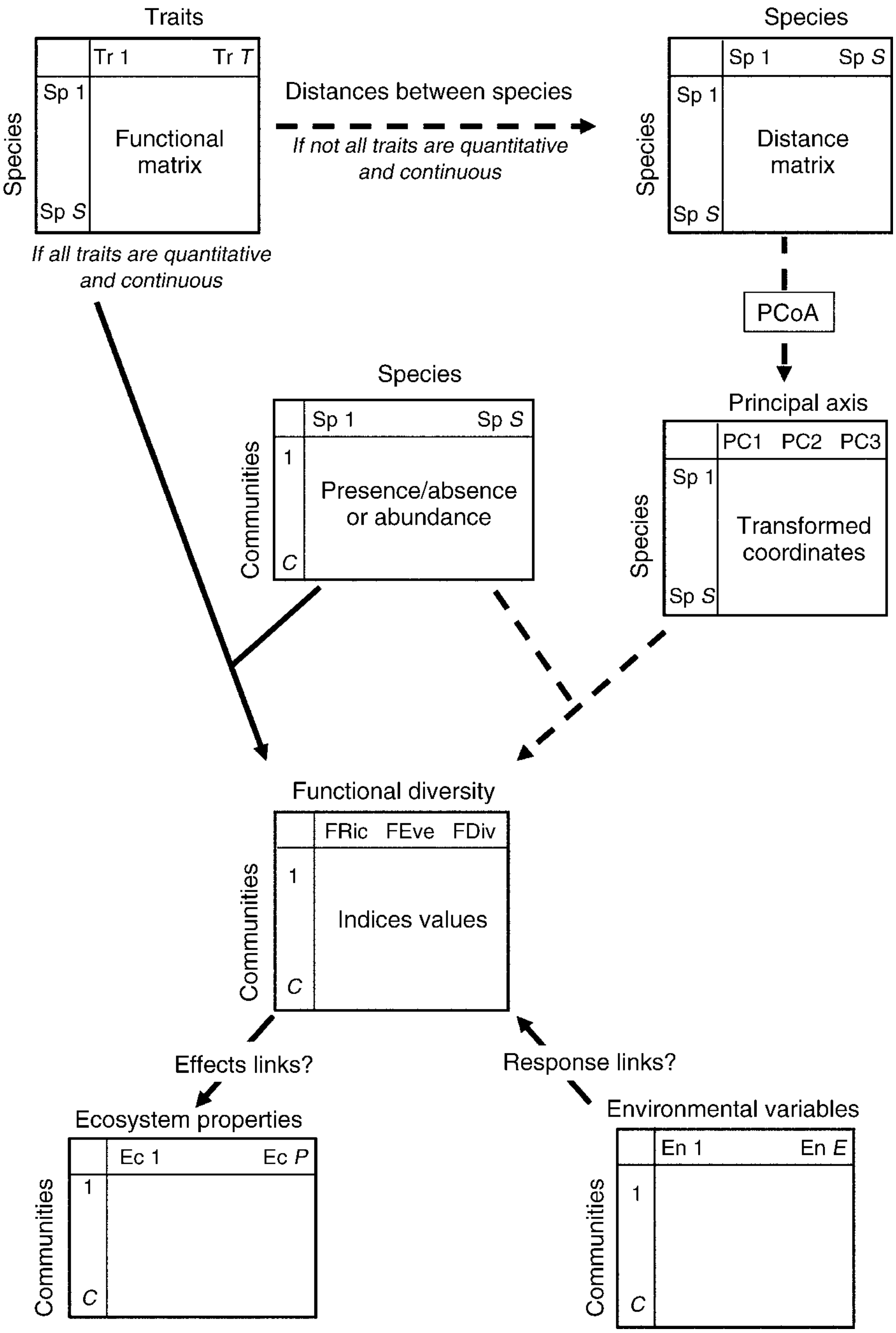

FIG. 5. General framework to study the effect of environmental conditions on functional diversity or the effect of functional diversity on ecosystem properties.

In summary, our set of three indices meets all the criteria required for functional diversity measures. The three indices are actually complementary. Moreover, functional divergence and evenness are independent from species richness, which allows comparison of communities with different species richness without bias. Similarly, their independence from functional richness allows for testing of differences in functional divergence or evenness with different functional richness values.

FROM THEORY TO PRACTICE

Generally, data sets contain two to four of the following matrices in Fig. 5: (1) a functional trait matrix (with values for each of the S species, for each of the T-functional traits), (2) an "abundance pattern" matrix (with the abundances of each species in the C communities), (3) an "environmental" matrix (with values for each of the E environmental variables in each community), and (4) an "ecosystem properties" matrix (with values for each of the P ecosystem properties such as productivity, flux of nutrients, or resistance to perturbation in each of the communities). The main limiting factor is that functional traits have to be the same for the communities to be compared. This emphasizes the need for consensual lists of traits for each type of organism (plant, terrestrial animal, fishes, microorganisms).

Moreover, as underlined by Petchey and Gaston (2006), the a priori selection of traits is often critical. The main problems concern the number of traits and their identity. Indeed, the number of traits is linked to the amount of work needed to measure them on each species, but also to the functions that are quantified. The choice of the traits has to be led by the need to describe each function as well as possible while avoiding redundancy (i.e., trivial correlations) between them. In particular, when using functional traits derived from other traits (e.g., ratios), original traits should not be used in calculating functional diversity since the original and derived traits may be trivially related. If traits are carefully selected, then any correlation between traits in the species–trait matrix may be considered a relevant aspect of species distribution in functional trait space. For example, the competitive, stress tolerant, and ruderal strategy (CSR) theory of Grime (1974, 2001) shows that correlations between traits that have no a priori link reveal major trends in plant functional strategy. More generally, correlations between traits may highlight patterns of species aggregation in a functional space where species separate into functional groups, whereas this may not be evident when functional traits are not correlated. Using ordination axes in calculating functional diversity will obscure these correlations. Ordinations also risk the loss of information, since the ordination axes can only capture a proportion of the variation in functional trait values across species. In summary, if functional traits are selected so that trivial correlations are avoided, any correlation between traits will represent a relevant aspect of species distribution in functional-trait space, and there will be no need to apply ordination techniques to obtain orthogonal axes. However, we may encounter constraints in the data which imply the use of ordination techniques, such as the use of too many traits compared to species number or the use of categorical data.

All of our indices are designed to quantify functional diversity using continuous traits. However, as exposed by Podani and Schmera (2006), ecological variables and, in particular, functional traits are sometimes qualitative either categorical (type of photosynthesis, ability to sprout after fire) or circular (time of reproduction). To overcome this problem, we propose to estimate a distance matrix using distances such the Gower distance which allows mixing qualitative and quantitative traits (Podani and Schmera 2006). In this case, a Principal Coordinates Analysis (PCoA) may be used to represent species distribution in a multidimensional functional space. PCoA works on distance matrix and its outputs are similar to those obtained from PCA (Legendre and Legendre 1998), i.e., the coordinates of species in a Euclidean functional space with reduced uncorrelated dimensions. Another particular case is the use of presence/absence data. Then, functional divergence and functional evenness have a different meaning in the sense that they would quantify the relative position of species within the functional space instead of the distribution of abundance.

However, we believe that in order to compare functional diversity values among communities with different species richness and different regional species pools, the best way is to consider observed values relative to those expected at random. Expected values may be obtained using a matrix swap randomization (Manly 1995) that maintains species richness of communities and the frequency of occurrence of species in randomized matrices. In fact, such a correction when comparing functional diversity of different local communities is necessary for all indices, since species functional traits in the pool will constrain the range of functional-diversity values possible. Methodologies for comparing observed functional diversity values to those expected by chance were provided in Mason et al. (2007, 2008).

The primary components of functional diversity identified by Mason et al. (2005) have aided us in finding a set of orthogonal multivariate functional diversity indices to give a comprehensive framework for the quantification of functional diversity in multidimensional functional trait space. It is possible that this framework does not capture all aspects of functional diversity, but it remains the sole available method for classifying functional diversity indices by the aspect of species distribution in functional trait space that they measure (cf. the classification system employed by Petchey and Gaston 2006). In helping to decide on a set of orthogonal indices, the primary functional diversity components aid the application of functional diversity indices in elucidation patterns and processes in ecological communities.

Functional diversity may act either as (1) an indicator of the processes governing community assembly (e.g., environmental and competitive filtering; Cornwell et al. 2006) and the impact of perturbations (e.g., climate change, fire, grazing or overfishing) and environmental gradients on community structure (e.g., Mouillot et al. 2007), or (2) an indicator of ecosystem functions such as productivity, resilience, and nutrient cycling (e.g., Petchey et al. 2004). Concurrent examination of functional diversity indices representing separate primary components increases the detail with which we may examine a variety of hypotheses relating to these dual roles of functional diversity. For example, Mason et al. (2008) found that functional evenness, compared to that expected at random, increased linearly with mean annual temperature and species richness in French lacustrine fish communities, while functional richness and functional divergence showed asymptotic relationships in both cases. These results, considered together, suggest that increased niche specialization (as opposed to an increase in the volume of niche space occupied) with increasing temperature allowed more species to coexist in high-energy communities. Similarly, an orthogonal set of indices might allow comparison of evidence for increased niche specialization or occupied niche volume as mechanisms for increased productivity or resilience. Using this approach, functional diversity indices may in effect be used to test not only whether niche complementarity enhances ecosystem function, but which type of complementarity enhances ecosystem function the most.

Until now, such an approach has been constrained to the use of univariate functional diversity indices. The three indices we propose here allow the implementation of the primary functional diversity components in multiple dimensions. They provide independent information about the position and relative abundances of species in a multidimensional functional space. Therefore, we believe that these new indices may help in the exploration of biodiversity–environment–ecosystem functioning relationships in ecology.

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Research

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Towards a consensus for calculating dendrogram-based functional diversity indices

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The widely used FD index of functional diversity is based on the construction of a dendrogram. This index has been the subject of a strong debate concerning the choice of the distance and the clustering method to be used, since the method chosen may greatly affect the FD values obtained. Much of this debate has been centred around which method of dendrogram construction gives a faithful representation of species distribution in multidimensional functional trait space. From artificially generated datasets varying in species richness and correlations between traits, we test whether any single combination of clustering method(s) and distance consistently produces a dendrogram that most closely corresponds to the matrix of functional distances between pairs of species studied. We also test the ability of consensus trees, which incorporate features common to a range of different dendrograms, to summarize distance matrices. Our results show that no combination of clustering method(s) and distance constantly outperforms the others due to the complexity of interactions between correlations of traits, species richness, distance measures and clustering methods. Furthermore, the construction of a consensus tree from a range of dendrograms is often the best solution. Consequently, we recommend testing all combinations of distances and clustering methods (including consensus trees), then selecting the most reliable tree (with the lowest dissimilarity) to estimate FD value. Furthermore we suggest that any index that requires the construction of functional dendrograms potentially benefits from this new approach.

Functional diversity has been identified as a key component of biodiversity for ecosystem functioning and sustainability (Ives et al. 1999, Hooper and Dukes 2004, Petchey et al. 2004). In this way, biodiversity loss can be responsible for a decrease in resilience or productivity (Loreau et al. 2001, Bellwood et al. 2004, Petchey 2004). Despite the emerging importance of the subject, no agreement exists about quantifying functional diversity of a community of species, though many indices have been recently proposed (reviewed by Petchey and Gaston 2006). Indeed, there has been a great deal of controversy over the statistical validity of these indices (Petchey and Gaston 2007, Podani and Schmera 2007) as well as their properties and what they actually measure (Ricotta 2005, Petchey and Gaston 2006). The FD index suggested by Petchey and Gaston (2002) provides an illustration of such controversy. FD is the total branch length of a functional dendrogram (hierarchical classification of the species according to their functional features). It measures functional diversity at all ecological scales simultaneously (Petchey and Gaston 2002), and is neither affected by units of characters nor by the splitting of a species into two identical functional species (Mason et al. 2003). Moreover, FD has been applied to a variety of taxa: mammals (Blackburn et al. 2005), plants (Thompson et al. 2005), birds (Petchey et al. 2007), fish (Mouillot et al. 2007) and zooplankton (Barnett et al. 2007), and the frequency of its use is likely to increase.

A dendrogram-based functional classification of species is carried out in three steps: (1) building the trait matrix (containing the value of each species for each functional trait); (2) calculating a matrix of distances between pairs of species in functional trait space; and (3) constructing a dendrogram to classify species according to the distance matrix (Petchey and Gaston 2002). The choices of the distance and of the classification method – steps (2) and (3) respectively – are of crucial importance since they may lead to different results.

Several distances are available in ecology (Bray–Curtis, Manhattan, etc). But Euclidean and Gower distances are the only two ones recommended to measure interspecific functional dissimilarity based on trait values. In fact, Petchey and Gaston (2002) employed Euclidean distance, while Podani and Schmera (2006) advised the use of Gower's distance (which allows missing data and inclusion of qualitative traits) even when all traits are quantitative.

There are also several clustering methods for constructing a hierarchical classification (Legendre and Legendre 1998). Each one of these methods is based on particular criteria to aggregate species into hierarchical clusters. The topology of the resulting tree varies according to the procedure employed for the same initial distance matrix. Consequently, numerical values of the total branch length of the dendrogram (i.e. FD) also depend on the distance and/or clustering algorithm used. However, there is a lack of agreement over which method of constructing the functional dendrogram gives the best representation of species distribution in functional trait space (Podani and Schmera 2006).

Thus, despite the broad use of the FD index, several questions remain to be answered. To what extent does the hierarchical classification represent the distribution of species in functional space? Which is the most faithful method of clustering? How can we improve the representation of the distance matrix by a hierarchical classification? Is there any factor influencing the performance of cluster algorithms? Does the same combination of distance and clustering method(s) always perform best? These questions are all crucial because the choice of a clustering method may strongly influence the functional diversity value obtained for a community. This problem was recently revealed by Podani and Schmera (2006). Indeed, no previous studies have quantitatively tested whether a single clustering method consistently outperforms all others. The choice of a clustering method remains arbitrary in functional ecology and no consensual solution has been yet proposed despite the popularity of FD.

In this paper, we present a novel procedure based on an objective criterion to choose the most appropriate method of constructing hierarchical dendrograms from functional trait data. This method aims to find the combination of distance and clustering algorithm(s) that best represents species distribution in functional trait space. Because each clustering algorithm has its flaws, we suggest also testing consensus trees resulting from a combination of several clustering algorithms to enhance the reliability of the classification and, ultimately, the estimation of functional diversity.

Material and methods

Hierarchical classifications synthesise the multidimensional distribution of objects (e.g. species, communities, assemblages) in a one-dimensional diagram. This procedure results in a loss of information about the dispersion of objects along each dimension summarized, resulting in distortion of data representation (Legendre and Legendre 1998). Our purpose is to find the least altered representation of species in a functional multidimensional space through a new method validated with simulated datasets.

Functional distance based on traits

To construct the distance matrix from artificial communities, we considered two distances. The Euclidean distance between species a and b for N quantitative traits was defined as:

$$ED_{ab} = \sqrt{\sum_{i=1}^{N} (x_{ia} - x_{ib})^2}$$

with x_{ia} and x_{ib} being the values of trait i (variable) for species a and b, respectively.

The Gower's distance can cope with mixed scale types of data (quantitative, interval, nominal or ordinal data, ratios, missing values). The general Gower's formula is given by:

$$GD_{ab} = \frac{\sum_{i=1}^{N} w_{iab} d_{iab}}{\sum_{i=1}^{N} w_{iab}}$$

where d_{iab} measures the dissimilarity between species a and b for the variable i:

$$d_{iab} = \frac{|x_{ia} - x_{ib}|}{\max(x_i) - \min(x_i)}$$

The weight $w_{iab} = 0$ when x_{ia} and/or x_{ib} is missing. In our framework, there was no missing value, trait values were all quantitative and each trait was equally weighted ($w_{iab} = 1$). Consequently, the formula was reduced to:

$$GD_{ab} = \frac{1}{N} \sum_{i=1}^{N} d_{iab}$$

Construction of a consensus tree

There are several clustering methods available for hierarchically clustering species into a dendrogram. In the present study, all methods tested belong to the family of hierarchical agglomerative (or ascending) classifications: single linkage, complete linkage, UPGMA, WPGMA, UPGMC, WPGMC and Ward's method (Table 1). Because clustering procedures fail to perfectly fit data distribution in multidimensional space, we tested whether using a consensus algorithm would enhance the faithfulness of dendrograms. Consensus algorithms make a synthesis from different dendrograms into one classification which highlights the concordant parts between the various methods relative to the parts that disagree (Darlu and Tassy 1993). In short, the algorithm builds the consensus tree that optimally represents several clustering methods. Several methods are available to form a consensus tree. The algorithm adopted here minimized the Euclidean distance between matrices (according to Gordon and Vichi 2001):

$$D_c = \sum_{j=1}^{n} d_{jc}$$

where d_{jc} is the Euclidean distance between the cophenetic distance matrix of dendrogram j and that of the consensus dendrogram c, and n is the number of individual dendrograms being considered.

Although the selected algorithm produces the best projection of the data according to its criteria, the quality

Table 1. Clustering methods tested (according to Legendre and Legendre 1998).

Clustering method	Acronym	Signification
Single linkage	SL	Fusion of the closest objects
Complete linkage	CL	Fusion of the most distant objects
Unweighted pair group method using arithmetic averages	UPGMA	Fusion of clusters when the similarity reaches the mean inter cluster similarity value
Weighted pair group method using arithmetic averages	WPGMA	Mean dissimilarity between two items is the sum of the weighted dissimilarities
Unweighted pair group centroid method	UPGMC	Fusion of the clusters with closest centroids
Weighted pair group centroid method	WPGMC	Fusion of the clusters with closest centroids after adjustment for group sizes
Ward's method	Ward	Minimization of the within-group sum of squares

of this representation can vary (contraction or dilation of space) according to the topology and the branch length of the resulting dendrogram. To assess the reliability of the dendrogram, we evaluated the dissimilarity between initial distance and cophenetic distance matrices, D_M, using the cophenetic correlation (Legendre and Legendre 1998). Cophenetic correlation has already been used by Blackburn et al. (2005) and Petchey et al. (2007) or discussed by Petchey and Gaston (2006, 2007) to evaluate the quality of the dendrogram which provided FD values. In this study, the dissimilarity value, D_M, is given by $1-c^2$; where c stands for the cophenetic correlation coefficient (Pearson correlation coefficient in our case). The objective was thus to identify, among all combinations of distance and clustering algorithm(s), the one that minimized the dissimilarity between the initial distance matrix and the cophenetic distance matrix ($D_M = 0$ corresponds to no distortion between distance matrices).

Theoretical datasets

To test this new flexible method in many different situations, we created artificial communities in order to control two parameters: species richness and correlation between functional traits. Because FD generally measures the functional diversity of a community using a dendrogram including all species present in the regional pool (hereafter called species assemblage) (Petchey and Gaston 2002), we defined two reasonable species richness levels for our simulated assemblages: 20 and 40 species. All artificial species assemblages were characterized by five simulated standardised functional traits sampled among a normal distribution with a mean of 5 and a standard deviation of 1. Traits were either forced to be all independent, or four of them were constrained to be highly correlated (Pearson correlation coefficient higher than 0.9) with the fifth being entirely independent of the others. We simulated one hundred assemblages for every combination of species richness levels and correlation levels (40 species with 5 independent traits; 40 species with 1 independent + 4 correlated traits; 20 species with 5 independent traits; 20 species with 1 independent + 4 correlated traits), giving a total of 400 artificial species assemblages.

Data analyses

The 7 'one-method' clustering algorithms and the 120 potential consensus trees (from 2 to 7 combined trees) multiplied by 2 distances made a total of 254 combinations of distance-clustering (consensus and 'one-method') algorithms that have been tested without any selection of methods, on each artificial assemblage. The D_M value of the 254 combinations was thus calculated for every species assemblage. Among all the 254 possible combinations of distances and clustering algorithms, the one with the lowest D_M value gave the most faithful picture of data distribution in space and thus was chosen as the most appropriate to calculate FD index. Then we retained the D_M value of the most reliable dendrogram (i.e. corresponding to the combination with the lowest dissimilarity) of every assemblage of each dataset to calculate the mean D_M of the sets. The significance of all main effects, and all possible interactions between factors (distances, clustering methods, correlations between traits and species richness) on DM were explored using a four factor ANOVA.

The effects of distances, clustering methods, correlations between traits and species richness on D_M were explored using a four factor ANOVA.

All calculations, including analyses of variances, datasets creation and tree constructions (consensus or not), were implemented using the R statistical environment (R Development Core Team 2006). Construction of consensus trees and dissimilarity tests were performed with, respectively, functions 'cl_consensus' and 'cl_dissimilarity' from the Clue package (Hornik 2005, Cluster ensembles, R package ver. 0.3–13). An R script is available from the authors to compute the different trees and to choose the most appropriate method (with the lowest dissimilarity) to built a functional tree.

Results

The effects of species richness, trait correlations, clustering methods and distances were estimated on the level of dissimilarity between initial distance and cophenetic distance matrices (D_M). The four factor ANOVA revealed that D_M varied significantly with the clustering method, the level of correlation among functional traits and species richness but the effect of distances was the less important (Table 2). Because most interactions were significant, the influence of single factors was, in general, dependent on the others. In other words, D_M was influenced by all the factors and their interactions. For example, when the traits were independent, the distance which provided the best tree (lowest D_M) was consistently Euclidean distance (with

Table 2. Effects of clustering methods, distances, levels of correlations between traits and species richness on dissimilarity D_M tested by a four factor ANOVA. F values with associated levels of significances (ns: non significant, *: $p<0.05$, **: $p<0.01$). (Cor: correlation; Met: clustering method; Dist: distance; SR: species richness; ×: interaction).

Factors	DF	F
Met	6	379.06**
Cor	1	3803.32**
SR	1	651.71**
Dist	1	12.25**
Met × Cor	6	32.67**
Met × SR	6	6.76**
Met × Dist	6	5.02**
Cor × SR	1	9.68**
Cor × Dist	1	247.72**
SR × Dist	1	5.29*
Met × Cor × SR	6	2.65*
Met × Cor × Dist	6	2.11*
Met × SR × Dist	6	0.91ns
Cor × SR × Dist	1	0.11ns
Met × Cor × SR × Dist	6	0.31ns

UPGMA) whereas, when they were correlated, Gower distance consistently provided the best result (still with UPGMA) (Fig. 1, Table 3a). Furthermore, higher species richness tended to decrease D_M (Fig. 1). However the number of clustering algorithms giving the lowest D_M value differed from one case to the other. For instance, the assemblage with the lowest D_M among the dataset 40 Indep (i.e. 100 assemblages of 40 species characterized by five independent traits) involved five clustering algorithms but only two algorithms in the other datasets 40 Cor, 20 Cor and 20 Indep (Table 3b). However, the complexity of interactions between factors made identification of the direct effects of each factor (distance measures, clustering algorithms, species levels, and correlations between traits) on D_M, difficult. Consequently, no combination of distance and clustering methods gave systematically the best representation of species from the multidimensional functional space. Each clustering algorithm and distance was, at least once, used in the best representation of data. Nevertheless, among all combinations, UPGMA/UPGMC consensus trees seemed to be most often used (Table 3a).

In addition, the comparison among dendrograms built with different combinations from the same sample (a 20 species assemblage characterized by five independent traits) illustrated the differences in species clustering provided by different combinations (Fig. 2). In our particular case, the lowest dissimilarity was obtained using the combination of Euclidean distance and consensus tree resulting from UPGMA/UPGMC/single linkage cluster algorithms ($D_M=0.27$, Fig. 2a). The combination Euclidean distance – UPGMA (Fig. 2b) obtained an intermediate dissimilarity level ($D_M=0.52$). The highest dissimilarity was given by the consensus tree WPGMC/Ward presented in Fig. 2c. In this case, the initial distance matrix (made with Gower's distance) had a dissimilarity value of 0.9 with the

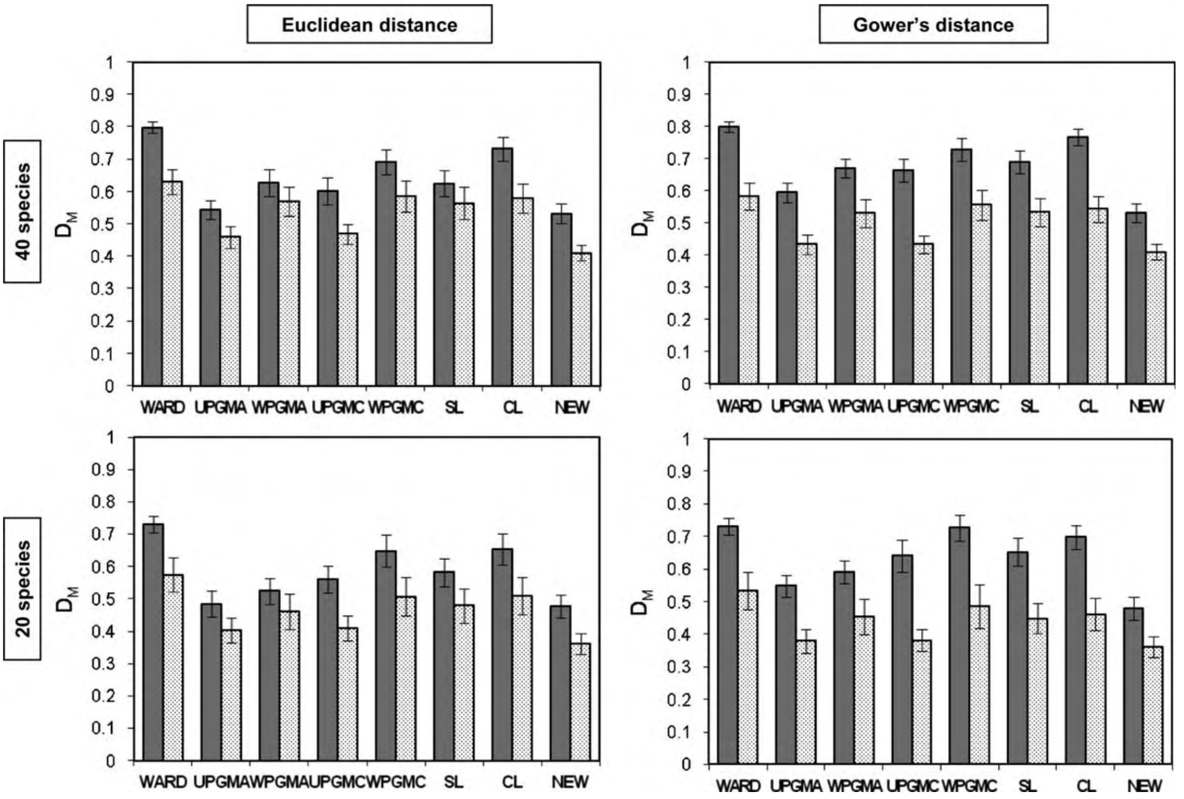

Fig. 1. Impact of clustering algorithms on dissimilarity. D_M values (y-axis) from 4 virtual datasets of 100 assemblages each. (WARD: Ward's method; SL: single linkage; CL: complete linkage; UPGMA: unweighted arithmetic average clustering; WPGMA: weighted arithmetic average clustering; UPGMC: unweighted centroid clustering; WPGMC: weighted centroid clustering; NEW: the new method proposed in this article). ■ Assemblages characterized by 5 independent traits. ░ Assemblages characterized by 4 correlated traits and 1 independent trait.

Table 3. Dissimilarity D_M tested on the best combination of distance – clustering algorithm(s) of each of the one hundred species assemblages of the four datasets. (a) Mean, D_{Mmean}, and standard deviation, D_{Msd}, of all datasets calculated with the dissimilarity value of the best combination of each assemblage, proportion of Euclidean and Gower distances involved in the best combinations and of the clustering algorithm(s) that gave the lowest dissimilarity in the greatest percentage of assemblages; (b) combination of distance – clustering method giving the lowest D_M of each species richness and trait correlation levels. (ED: Euclidean distance; GD: Gower's distance; 40 Indep: 40 species with 5 independent traits; 20 Indep: 20 species with 5 independent traits; 40 Cor: 40 species with 1 independent+4 correlated traits; 20 Cor: 20 species with 1 independent+4 correlated traits).

(a)

Datasets	D_{Mmean}	D_{Msd}	Distances	Clustering algorithms
40 Indep	0.533	0.059	ED: 94.1% GD: 5.9%	UPGMA–UPGMC: 34%
20 Indep	0.478	0.07	ED: 90.9% GD: 9.1%	UPGMA–WPGMC: 22%
40 Cor	0.411	0.05	ED: 11.4% GD: 88.6%	UPGMA–UPGMC: 35%
20 Cor	0.361	0.066	ED: 20.8% GD: 79.2%	UPGMA–UPGMC: 24%

(b)

Datasets	D_M	Distances	Clustering algorithms
40 Indep	0.386	ED	UPGMA – UPGMC – CL – WPGMA – SL
20 Indep	0.295	ED	UPGMA – WPGMC
40 Cor	0.275	GD	UPGMA – SL
20 Cor	0.195	GD	UPGMA – UPGMC

cophenetic distance matrix of the tree. Some strong inconsistencies appeared between these three dendrograms (Fig. 2). For instance, the position of species 1 changed drastically among dendrograms. Species 1 was joined together with species 3 using Euclidian distance and UPGMA cluster algorithm while this species was associated to the couple of species 2–5 according to the consensus tree combining UPGMA/UPGMC/single linkage methods. However, the results obtained from the initial distance matrix (here, Euclidean) showed that distance $ED_{1-3} = 5$ was higher than the distances $ED_{2-1} = 4.51$, and $ED_{5-1} = 3.61$. Thus, species 1 was more distant in functional trait space from species 3 than from species 2 and 5, indicating that some methods may incorrectly classify species 1 and 3 together.

Discussion

Indices based on a hierarchical classification are highly dependent on the capacity of the clustering method to accurately represent the distribution of species in a functional space (Podani and Schmera 2007). This critical point deserves to be quantitatively studied. From artificially generated data, we have tested whether any single of seven clustering methods and two distances always performs better than the others, or if it is necessary to choose a "consensus" dendrogram. Taken together (Fig. 1, Table 2, 3), our results show (1) that the characteristics of the species assemblages inconsistently influence the performance of the methods, (2) that there is no general rule for the choice of a distance or a clustering method and (3) that the best representation is often provided by a consensus tree.

Rao and Srinivas (2006) defined a threshold for validity of a dendrogram: the dissimilarity between initial distance and cophenetic distance matrices, D_M, must be less than 0.36 (corresponding to the 0.8 correlation coefficient limit stated by Rao and Srinivas). Some algorithms are well known to cause a distortion of space (Legendre and Legendre 1998). Single linkage tends to contract space by compressing edges of the dendrograms whereas complete linkage tends to dilate data space to produce compact classes (Podani and Schmera 2006). Despite their drawbacks, single linkage and complete linkage must not be ignored because they are regularly included in the consensus trees yielding the lowest D_M (Table 3b). Dendrograms built using the UPGMA method give the lowest D_M values (Fig. 1), that is a better representation of data. Among the algorithms selected in the study, UPGMA is a good compromise between single linkage and complete linkage because it preserves most of the initial distances in dimensionally reduced space. In contrast, the Ward's method, though widely used, produces the least reliable classifications (Fig. 1). Nevertheless, hierarchical classifications are one-dimensional pictures of data dispersed in an n-dimension space. So, none of the clustering algorithms (even UPGMA) perfectly corresponds to the distribution of objects in a multidimensional space. As demonstrated here, the quality of representation offered by clustering methods is also modulated by other factors: level of correlations between traits and species richness (Table 2). Therefore, it is worth gathering information from different clustering methods into consensus trees.

To evaluate the faithfulness of a hierarchical classification, the method presented here relies on cophenetic correlation through a dissimilarity measure (D_M). Cophenetic correlation quantifies the agreement between the initial distance matrix and the cophenetic distance matrix. In other words, cophenetic correlation enables one to choose the best combination of clustering method according to the distance employed. However cophenetic correlation does not take into account the transformation of the trait matrix into a distance matrix. More studies are needed to assess the impact of that transformation and of the use of other distances (Manhattan, Bray–Curtis, etc.). Besides, the faithfulness of a classification may decline with a decrease in the number of functional traits and/or species richness (Sokal et al. 1992).

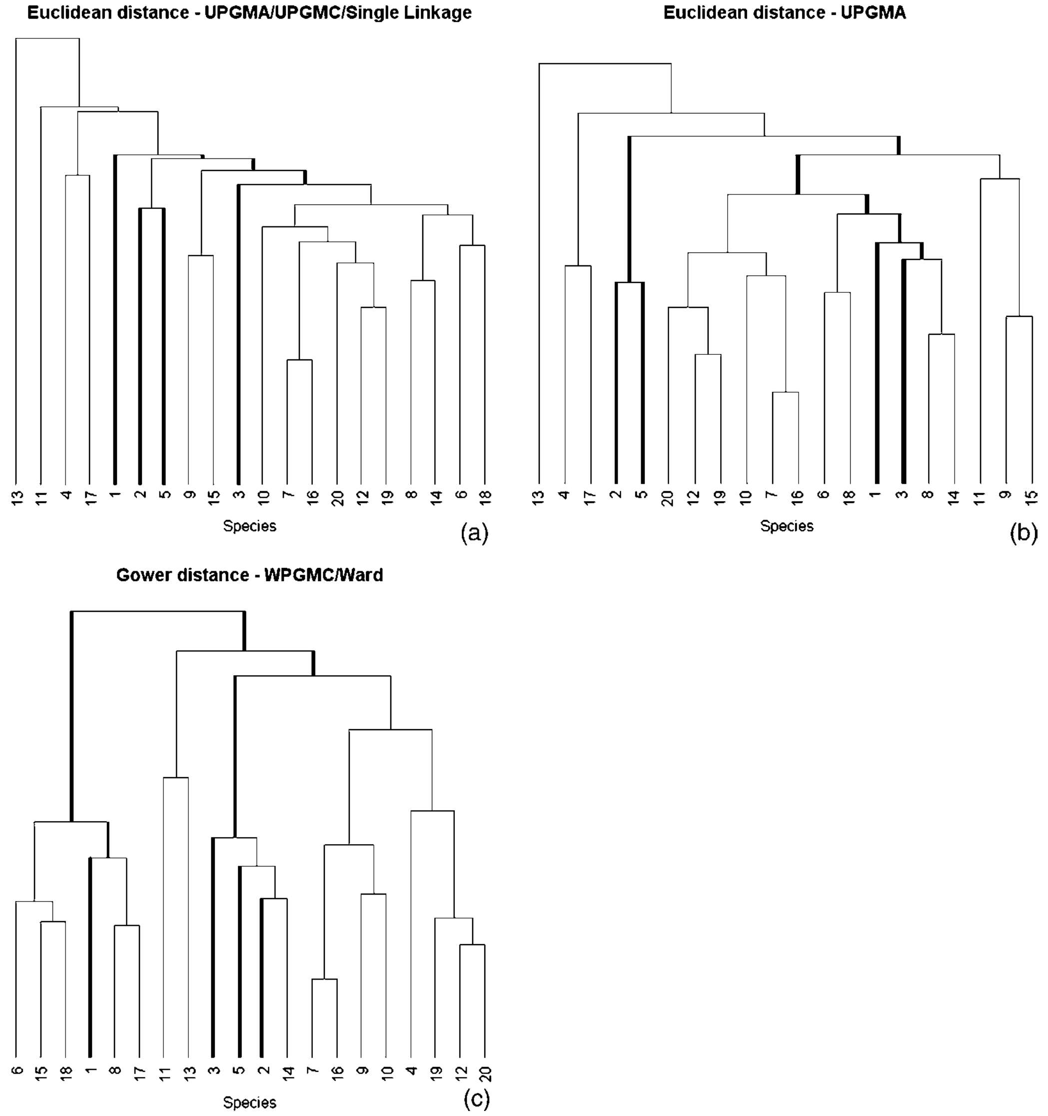

Fig. 2. Hierarchical classifications of an artificial species assemblage composed of 20 species characterized by 5 independent functional traits. (a) with the lowest D_M ($D_M = 0.27$); (b) with an intermediate D_M ($D_M = 0.52$); (c) with the highest D_M ($D_M = 0.9$).

The debate on the calculation of index FD originates from the difficulty of choosing the right combination of distance-clustering method (Podani and Schmera 2006). Our results show that there is not a unique answer, each case being different because of the complexity of interactions between factors such as correlations of traits, species richness, distances and clustering methods. For instance, the choice of the distance is not only related to the type of data. Even if Gower's formula is the only way to cope with mixed data, Euclidean distance must not be excluded when all data are quantitative (Fig. 1). Overall, in our results, the best solution is often given by a consensus tree combining dendrograms produced using several different clustering algorithms. Consensus trees increase the quality of representation of the species on the dendrogram (Fig. 1). They minimize the dissimilarity with the initial distances and preserve the parts common to several trees. As a consequence, FD values obtained will be more accurate. Nevertheless, if the less distorted representation is still very dissimilar from the original distance matrix, FD should not be measured to avoid erroneous interpretations about the functional structure of a community.

Alternatively, we advise against making any a priori choice of a distance or a clustering algorithm but, instead, we propose testing all the possible combinations (including consensus trees) and selecting the one with the lowest dissimilarity value to estimate FD. The choice of the method is therefore objective. Searching for the best combination of distance and clustering algorithm(s) is a good answer to the debate around FD's statistical validity. In addition, our method potentially has a broader 'field' of application than the calculation of index FD. Indeed, the simple classification of species into functional groups is still largely subjective since many alternatives exist for the clustering algorithm. This lack of agreement may weaken the conclusions about the role of functional diversity on ecosystem functioning (Wright et al. 2006). The investigation of the relationship between the shape of functional dendrograms and the patterns of species relative abundances would also benefit from such an objective tool (Sugihara et al. 2003). Finally, the calculation of indices that require the construction of dendrograms to obtain ultrametric distances among species pairs, such as the originality of a species (Pavoine et al. 2005) or the 'turn-over' of communities along environmental gradients (Hardy and Senterre 2007), could also benefit from this method.

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MANUSCRIT D

Redundancy and complementarity in functional diversity estimators

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Abstract

Indices quantifying the functional aspect of biodiversity are essential in understanding the relationships between biodiversity, ecosystem functioning and environmental constraints. Many indices of functional diversity have been published but we still lack consensus about what they quantify and which ones are recommended. Statistical properties and biological meaning of these estimators are the subject of intense debate. The aim of this study is to build a typology of functional diversity indices from artificial data sets encompassing various community structures (species richness and trait correlations) and then to identify a set of independent and unbiased indices. Our results confirm that functional diversity indices can be divided into three groups, each of these corresponding to one aspect of functional diversity: functional richness, functional divergence and functional evenness. Most of indices are highly correlated and quantify functional richness while the quadratic entropy (Q) represents a mix between functional richness and functional divergence. At the opposite, two indices (FEve and FDiv respectively quantifying functional evenness and functional divergence) are independent to all the others. To accurately assess functional diversity and establish its relationships with ecosystem functioning, we recommend investigating each functional component separately with the appropriate index.

Keywords: Functional richness, functional evenness, functional divergence, artificial data, trait correlation, ecosystem functioning.

Introduction

Biological diversity, or biodiversity, defined as “the variety of life on Earth at all its levels, from genes to ecosystems, and the ecological and evolutionary processes that sustain it” (Gaston 1996), embraces the diversity of genes, phenotypes, populations, species, communities and ecosystems. As a result, quantifying such a broad concept has proved to be problematic. However, as Purvis and Hector (2000) highlighted, “We cannot even begin to look at how biodiversity is distributed, or how fast it is disappearing, unless we can put units on it”. Classical biodiversity measurement (species richness or the myriad of diversity indices such as Shannon) relied on three main assumptions: (1) all species are equal (only relative abundances establish the relative importance of species), (2) all individuals are equal (whatever their size) and (3) species abundance has been correctly assessed with appropriate tools and in similar units (Magurran 2005). Yet, species not only offer a wide range of colors or life forms to the Human eye, they are also likely to support many goods and services through ecosystem processes (e.g. Díaz et al. 2007). Hence, the first assumption of biodiversity measurement is not valid: species are not equal in their effects on ecosystem functioning since their functional traits matter to ecosystem processes (e.g. Mokany et al. 2008).

As early as 1994, Solow and Polasky suggested that measuring diversity was equal to characterizing the distribution of points in space. Accordingly, measuring functional diversity is quantifying the distribution of functional units in a multidimensional space (Villéger et al. 2008). By analogy with Hutchinson’s niche, Rosenfeld (2002) defined functional diversity (i.e. the functional component of biodiversity) as the distribution of species in a functional space whose each axis represents a functional feature or an environmental gradient. A new generation of measurements has already been proposed to quantify this multidimensional distribution (see Petchey and Gaston 2006 for a review). In spite of the importance of the subject, there is no consensus on how quantifying the functional diversity of a community and relationships between the various indices have not been established.

Mason et al. (2005), in suggesting that functional diversity could be divided into three primary components - functional richness, functional divergence and functional evenness - proposed a definition of functional diversity to guide the conception of new indices and for categorizing existing ones. This decomposition of functional diversity reflects complementary characteristics of abundance distribution of taxa (or individuals) in functional space. Linking indices to a particular functional diversity component could greatly aid ecologists in deciding on a minimum set of indices from the ever increasing range of options. Since each component describes an independent aspect of functional diversity, any study quantifying functional diversity should include at least one index for each component. Previous works have already categorized functional diversity indices (Petchey et al. 2004, Ricotta 2005, Petchey and Gaston 2006). Among concluding remarks, Petchey and Gaston (2006) emphasized the necessity to determine which functional diversity measure performs best. Formerly, the explanatory power and their statistical validity have to be well defined. For example, an increase in species richness and/or co-linearity between traits may modify the behavior of each index. Correctly identifying bias in index calculation is crucial to avoid spurious conclusions. Furthermore, no study clearly establishes which measures estimate which facet of functional diversity and several meanings have been attributed to the same index. For instance, the Rao's quadratic entropy (Q) either measures functional diversity (Lepš et al. 2006, Scherer-Lorenzen et al. 2007, Weigelt et al. 2008) or functional divergence (Díaz et al. 2007, Lavorel et al. 2008). It thus becomes critical to evaluate the possible redundancy or complementarity between these various indices. In other words, do functional diversity indices all quantify the same facet of functional diversity? The principal objective of this study is therefore to set up the typology of existing functional diversity indices, to determine their validity according to relevant criteria, and to evaluate their ability to describe one of the primary functional diversity components.

Material and methods

Functional diversity estimators

One of the first methods proposed to quantify functional diversity relies on the distribution of species into various functional groups according to an *a priori* classification (Hooper and Vitousek 1997, Tilman et al. 1997). The number of functional groups is assumed to evaluate species complementarity in resource use (Petchey 2004). However, the choice of functional groups is not based on objective (mathematical or statistical) methods. Indeed, the threshold, from which functional interspecific dissimilarities are considered to be significant, is an arbitrary decision of the experimenter (Wright et al. 2006). This underlines the necessity to work with continuous and objective measurement of functional diversity (Petchey et al. 2004).

The first published index measuring functional diversity in a continuous way, Functional Diversity Attribute (FAD, Walker et al. 1999), quantified the sum of all functional pairwise distances between species belonging to the same community. This index evaluates the average functional contribution of each species to the total diversity of a community (Ricotta 2005). In a step forward Petchey and Gaston (2002) proposed the FD index which measures functional diversity from the total branch length linking species belonging to the same community on the functional dendrogram built on the regional pool of species. Then, Botta-Dukát (2005) advised the use of Rao's quadratic entropy (according to Rao 1982) as a functional diversity estimator.

Table 1. Functional diversity measures

Index		Description	Formule	Based on	Abundances included
Functional Divergence (Villéger et al. 2008)	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + \overline{dG}}$	Trait values	Yes
Functional Evenness (Villéger et al. 2008)	FEve	Sum of MST branch length weighted by relative abundance	$FEve = \frac{\sum_{l=1}^{S-1} \min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Trait values	Yes
Functional Richness (Villéger et al. 2008)	FRic	Convex Hull Volume	Quickhull algorithm	Trait values	No
Rao's quadratic entropy (according to Rao 1982)	Q	Sum of pairwise distances between species weighted by relative abundance	$Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j$	Distance matrix	Yes
Functional Attribute Diversity (Walker et al. 1999)	FAD	Sum of pairwise distances between species	$FAD = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}$	Distance matrix	No
Modified Functional Attribute Diversity (Schmera et al. 2008)	MFAD	Sum of pairwise distances between functional units	$MFAD = \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} d_{ij}}{N}$	Distance matrix	No
Functional Diversity (Petchey and Gaston 2002)	FD	Sum of branch length of a functional classification	$FD = i' \cdot h2$	Hierarchical classification	No
Generalized Functional Diversity (Mouchet et al. 2008)	GFD	Sum of branch length of a functional classification	$GFD = i' \cdot h2$	Hierarchical classification	No

(d_{ij}: dissimilarity between species (or functional unit) i and j (with S, the total species richness or N, the total number of functional units). p_i: relative abundance of species i. x: trait value. $\overline{dG}$: mean distance to the centre of gravity from the centre of gravity. Δd: sum of abundance-weighted deviances. $\Delta\lvert d\rvert$: absolute abundance-weighted deviances from the centre of gravity. *PEW:* partial weighted evenness. i' : branch presence/absence row vector; $h2$, branch length vector).

Following the functional diversity decomposition of Mason et al. (2005), several measurements have been presented to assess each facet: FDvar (Mason et al. 2003), a measurement of the functional divergence (previously proposed as a functional diversity index) and an index of functional richness RF (Mason et al. 2005). In parallel, Mouillot et al. (2005) quantified the functional regularity (or evenness) with FRO. FDvar, as well as RF and FRO, is a univariate index (e.g. only one functional trait taken into account). More recently, Villéger et al. (2008) defined multivariate measurements for functional diversity components: FRic (functional richness), FEve (functional evenness) and FDiv (functional divergence). Concurrently, two modified version of previous functional diversity FD and FAD have been proposed: GFD (Mouchet et al. 2008) and MFAD (Schmera et al. 2008), respectively. To fit Rosenfeld's definition of functional diversity, we chose to only study multivariate measures. Descriptions, calculations and references of the eight selected indices FRic, FAD, MFAD, FD, GFD, Q, FDiv and FEve are presented in Table 1.

Theoretical datasets

We created artificial communities in order to control species richness, the range of functional traits and their correlations. Ten species richness levels were considered (from 10 to 100 species with an interval of 10). All artificial communities were simulated using five standardised functional traits sampled in a uniform distribution (range = 10) to investigate index behaviors. We also defined three different levels of correlation between functional traits: random (to establish a typology), highly correlated (four correlated traits, Spearman correlation coefficient above 0.85, and one totally independent from the others) and independent (Spearman correlation coefficient below 0.15 between each pair of traits) (to test properties of the measures). Species abundances, randomly assigned to species, were generated using a uniform distribution within a range of 100 and then standardised to relative abundances. We simulated one hundred communities for every species richness level giving a total of 1000 artificial species communities per correlation level between traits.

Typology of the functional diversity indices

Each index of functional diversity was calculated for one thousand artificial communities characterized with functional traits randomly correlated to each other. The relationships between each pair of functional diversity measures were investigated using the Spearman correlation coefficient. Then a typology of all indices was carried out on the matrix crossing functional diversity estimators (variables) and communities (objects) thanks to a Principal Components Analysis (PCA). To support the classification of indices in various groups following the PCA, we applied a K-means partition (Legendre & Legendre 1998) based on index coordinates on the main PCA axes (i.e. those with an eigenvalue higher or equal to 1). For each number of groups, the Calinski-Harabasz criterion (1974) was computed. This criterion uses the Variance Ratio Criterion, which is analogous to F-Statistics, to minimize the within-group sum of squares and maximize the between-group sum of squares. The number of groups yielding the highest Calinski-Harabasz value corresponds to the most compact set of groups.

Properties of the indices

We examined the influence of two major parameters on multivariate functional diversity indices: species richness and correlation between functional traits. The relationship of each measure of functional diversity with species richness was explored using Spearman correlation tests. The impact of functional space dimensionality on measurements was also investigated using theoretical samples whose traits were forced to be independent from one another (each trait provides independent information) or highly correlated (highly correlated traits summarized the same information). Finally, a set of criteria from Mason et al. (2003) and Ricotta (2005) were examined to define the pros and cons of every measure.

Results

Partitioning functional diversity measures

Spearman correlation between functional diversity measures (Table 2) revealed a high correlation between FRic, FAD, MFAD, GFD and FD (coefficient values from 0.89 to 0.99 and $p<0.001$). The highest correlation values were obtained for the pairs FD-FAD, FRic-FD and FRic-FAD with, respectively, a Spearman correlation of 0.99, 0.98 and 0.98. As expected, GFD and FD on one hand, MFAD and FAD on the other hand, are highly associated (Spearman coefficients of 0.92 and 0.98, respectively). FEve and FDiv proved to be weakly correlated to other measures (see Table 2 for details). Finally, Q, was essentially related to FRic ($r_{\text{Q-FRic}}=0.60$, $p<0.001$) and FDiv ($r_{\text{Q-FDiv}}=0.45$, $p<0.001$).

Table 2. Spearman correlation coefficients between functional diversity estimators The correlation coefficients are evaluated on 1000 artificial species communities, characterized by randomly correlated functional traits, scattered into ten species richness levels.

	FRic	FAD	MFAD	GFD	FD	Q	FDiv	FEve
FRic	1							
FAD	0.98***	1						
MFAD	0.96***	0.98***	1					
GFD	0.89***	0.92***	0.90***	1				
FD	0.98***	0.99***	0.97***	0.92***	1			
Q	0.60***	0.54***	0.52***	0.42***	0.51***	1		
FDiv	0.08*	0.09**	0.09**	0.05^{NS}	0.07*	0.45***	1	
FEve	-0.31***	-0.29***	-0.30***	-0.29***	-0.29***	-0.17***	-0.03^{NS}	1

^{NS} non significant, * significant, ** highly significant, *** very highly significant.

The Principal Component Analysis, whose first three axes accounted for 91.23% of total inertia, was carried out on the eight indices (Figure 1). The method of K-means classification confirmed the classification of indices into four groups (Calinski-Harabasz criterion=238.45). The first group gathered FRic, MFAD, FAD, FD and GFD. The second group was composed of Q, the third one of FDiv and the last group included FEve.

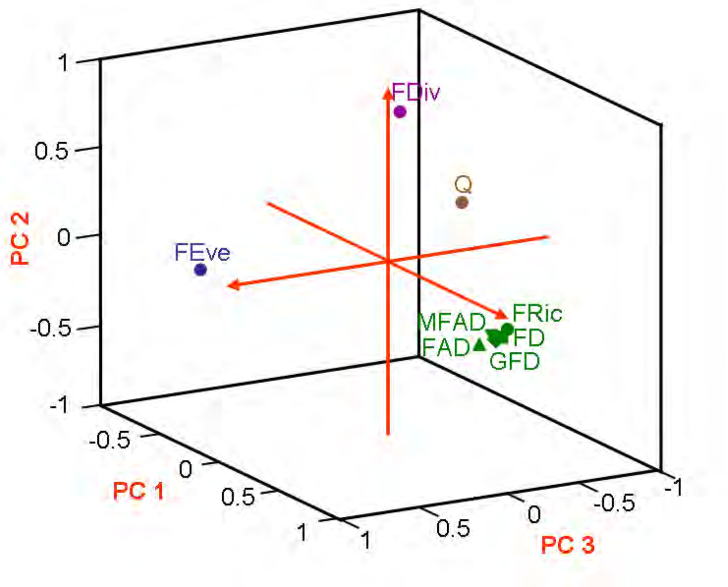

Figure 1. Principal Component Analysis carried out on 1000 artificial species communities, characterized by randomly correlated functional traits and random species abundances, dispatched into ten species richness levels (10, 20, 30, 40, 50, 60, 70, 80, 90, 100 sp). The first three axes accounted for 91.23% of total inertia: PC1, PC2 and PC3 accounted for 64.51%, 15.11% and 11.61% of the total variation. The 8 functional diversity indices are represented in the three axes volume. Colors disentangle K-means groups: functional richness indices in green, functional evenness index in blue, functional divergence index in purple and Rao's quadratic entropy in brown.

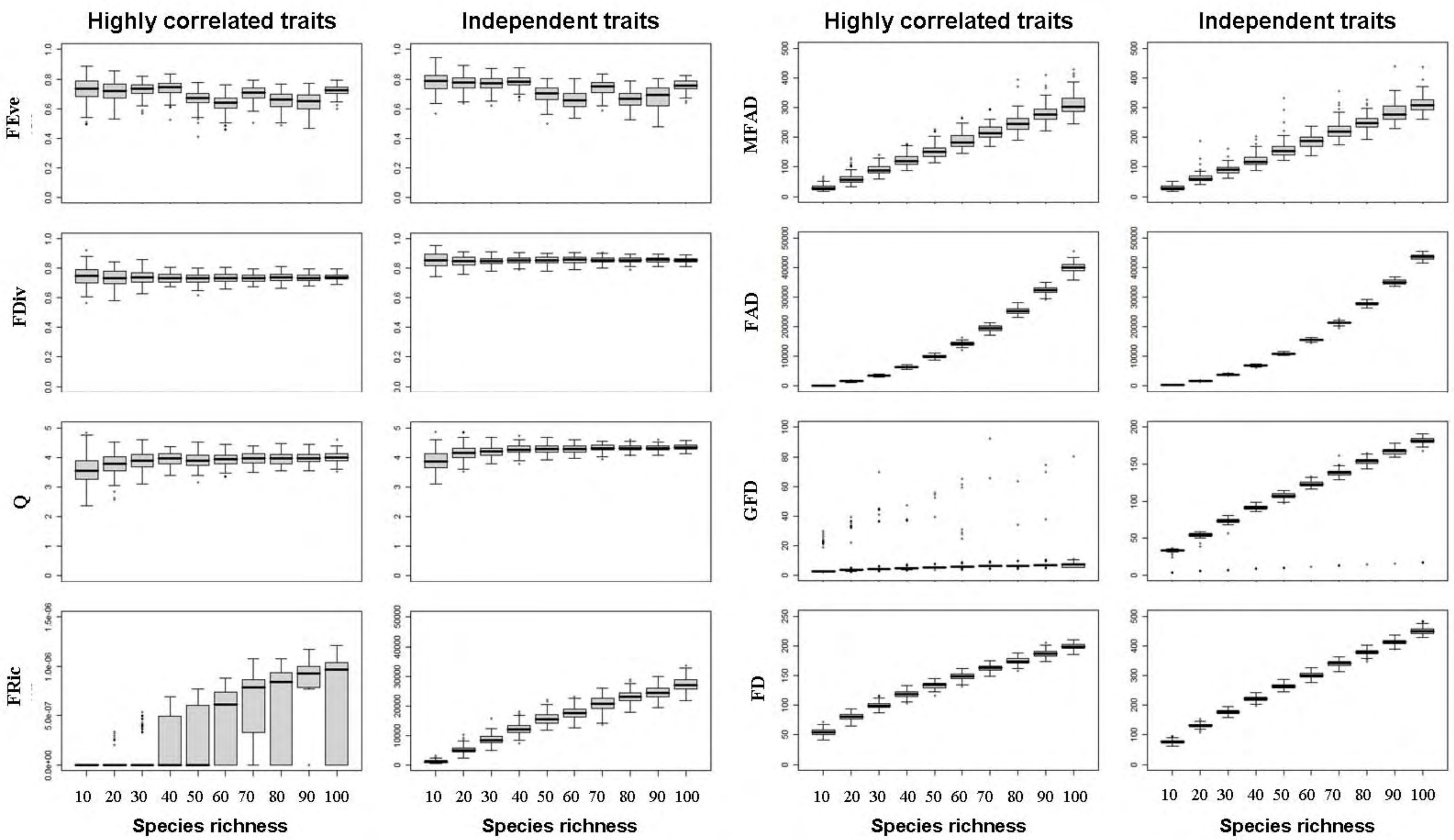

Figure 2. Functional diversity indices as a function of species richness for two levels of trait correlation.
“Highly-correlated-traits” communities: four correlated traits (Spearman correlation coefficient above 0.85) + one totally independent from the others.
“Independent-traits”: Spearman correlation coefficient below 0.15 between each pair of trait

Properties of functional diversity indices

FRic, MFAD, FAD, GFD and FD were highly correlated to species richness (Spearman correlation coefficients of $r_{FRic}=0.97$, $r_{MFAD}=0.97$, $r_{FAD}=0.99$, $r_{FGFD}=0.92$, $r_{FD}=0.92$, $p<0.001$ for all). In contrast, Q was less dependent on species richness ($r_Q=0.47$, $p<0.001$) whereas FDiv and FEve were weakly, albeit significantly, dependent of species richness (respectively, $r_{FDiv}=0.07$ and $r_{FEve}=-0.3$). Correlation between traits strongly influenced GFD, FD and FRic ranges whereas the ranges of Q, MFAD, FAD, FEve and FDiv indices were unchanged (Figure 2).

Discussion

Species richness impact

Among all measures of functional diversity, only indices of functional richness (MFAD, FAD, GFD, FD and FRic) are sensitive to the variations of species richness. In fact, the probability of occupying a broader functional space increases with the number of species by sampling effects. In the case of FAD, the addition of a species is accompanied by the addition of new pairwise distances, whatever the degree of functional redundancy with the species already present in the community. This drawback is partially solved by MFAD. MFAD is calculated on functional units: two functionally redundant species are considered as one (Ricotta 2005, Schmera et al. 2008). Unfortunately, no species is entirely redundant with another when continuous and quantitative data are considered. So the functional unit is no longer relevant, FAD and MFAD have an identical relationship to species richness and the species splitting remains problematic. Even if the relation is weak because of the abundance weighting, Q is also sensitive to species richness. On the other hand, functional divergence and evenness estimators, respectively FDiv and FEve, are weakly sensitive to species richness according to their construction (Villéger et al. 2008).

Correlation between functional traits

The functional niche is defined by functional traits. Accordingly, a high correlation among traits provokes a drop in the functional space dimensionality (all traits are redundant). Correlation between functional traits only interacts with functional richness indices (FRic, MFAD, FAD, GFD and FD). FRic and GFD are the most affected indices by the level of correlation between traits. Even if the range of FD values decreases by half for correlated traits relative to uncorrelated traits, the shape of the FD–species richness relationship remains quite similar. This is to be expected as only expansion of the occupied volume of functional space causes an increase in FRic, while any functional difference will cause an increase in FD. This sensitivity to small functional differences between species means that FD will generally increase quasi-linearly with increasing species richness, and consequently supplies little independent information from species richness except using null models (Petchey et al. 2007). In both cases MFAD and FAD increase exponentially with species richness, indicating that this index is highly sensitive to species richness. MFAD and FAD are based on unweighted pairwise distances and do not correctly translate the degree of redundancy among species or traits (see *Species richness impact* for further explanations). Functional richness is very sensitive to the dimensionality of functional space, and thus to correlations among traits. Among functional richness estimators, only FRic and GFD accurately represent the change in functional space dimensionality. FEve, FDiv and Q are independent of the correlation between traits. Functional evenness and divergence, through FEve and FDiv, quantify the distribution of functional units in functional space whatever the number of dimensions of the functional niche.

Facets of functional diversity

Functional diversity components (richness, divergence, evenness) were already presented in a univariate framework (Mason et al. 2005, Mouillot et al. 2005) but our approach, based on simulated communities and mixing existing indices, proves that three orthogonal functional components can be discriminated. Not all functional diversity estimators measure the same aspect of functional diversity but some are redundant. The first component of functional diversity, functional richness, is characterized by a group of indices having common properties. It gathers FRic, MFAD, FAD, GFD and FD indices which quantify the volume occupied by the species in functional space (biomass is not involved). Functional richness indices give no information on functional redundancy and none on biomass distribution. The second of these components (functional divergence) is represented by FDiv. The maximization of dissimilarities between functional species (and their relative abundances) defines the degree of functional divergence independently of functional richness. Indeed, FDiv was designed to be independent from the volume of functional space occupied (Villéger et al. 2008). The last of these components, functional evenness, is represented only by FEve. FEve measures the regularity of the distribution of biomass in functional space.

Q is the only functional diversity measure that is not clearly related to one of the functional diversity components. In fact, Q is not merely a measure of functional divergence. Weigelt et al. (2008) characterized Rao's quadratic entropy Q as "a continuous measure of functional diversity including information about the evenness of the distribution of functional traits within a community”. Besides, Scherer-Lorenzen et al. (2007) found a strong correlation between FD and Q (Pearson correlation coefficient of 0.73). Here we demonstrate that Q is not fully associated to one of the two components described previously. Indeed, both PCA and Spearman correlation coefficients prove that Q embraces two components: functional richness and divergence. This arises since Q increases both when species become more distant in functional trait space and when species with extreme trait values have high relative abundances. No one functional diversity measure encapsulates the three facets simultaneously. Investigation of functional diversity must consider the three independent components of functional diversity to improve our comprehension of the relationships between environment, biodiversity and ecosystem functioning (see Villéger et al. (2008) for a complete framework).

Which functional diversity measure to choose?

No one index can fulfill all Mason et al. (2003) and Ricotta (2005) criteria (Table 3).

Table 3. Criteria for classifying functional indices (from Mason et al. 2003 and Ricotta 2005)

Criteria	FRic	FDiv	FEve	Q	FAD	MFAD	FD	GFD
Positive values*°	YES	YES	YES	YES	YES	YES	YES	YES
Be constrained to a 0 -1 range (for convenience) and use that range well*	NO	YES	YES	NO	NO	NO	NO	NO
Be unaffected by the units in which the abundance is measured*	YES	YES	YES	YES	YES	YES	YES	YES
Reflect the contribution of each species in proportion to its abundance*	NO	YES	YES	YES	NO	NO	NO	NO
Be unaffected by the units in which the character is measured*	NO	YES	YES	NO	NO	NO	NO	NO
Reflect the range of character values present*	YES	NO	NO	YES	YES	YES	YES	YES
Be unaffected by the number of species*	NO	YES	YES	YES	NO	YES	NO	NO
Set monotonicity (a subset of a community is less diverse than this community)°	YES	NO	NO	NO	NO	YES	YES	YES
Concavity (a set of communities is, in mean, less diverse than the aggregated pool)°	YES	NO	NO	YES	YES	YES	YES	YES
Unaffected by split*°	YES	NO	NO	YES	NO	YES	YES	YES

*criterion proposed by Mason et al. 2003, °criterion proposed by Ricotta 2005

Functional diversity should better be quantified in a multidimensional functional space where each functional facet (richness, divergence and evenness) is measured by an estimator. FAD and MFAD are sensitive to the splitting of a species into two functionally identical species. The FD index (Petchey and Gaston 2002) is insensitive to species splitting but is influenced by the distance metric and the clustering algorithm chosen (Podani and Schmera 2006). In order to ignore the bias, Mouchet et al. (2008) suggested testing the influence of the distance and clustering algorithm and then objectively choosing the hierarchical dendrogram that most closely represents pairwise distances between species. Therefore, GFD better fits the data structure. When redundancy among species is high, GFD is much lower than FD. GFD more accurately translates similarities among species.Still, dendrogram-based measures GFD and FD rely on dimension reduction methods leading to a loss of information and a potential bias in functional diversity estimation if the tree representation does not match species' distribution in functional space (Mouchet et al. 2008). FRic is based on the convex hull volume (Cornwell et al. 2006). Consequently, FRic is neither manipulated by split nor by dendrogram bias but depends on the species being vertices. However, FRic computation needs more species than trait axes. In sum, FRic is the most suitable functional richness index but GFD represents a relevant alternative in case of mixed data (i.e. including categorical and quantitative traits) or when the number of functional traits is greater than species richness. FEve and FDiv are the only multivariate measurements available for, respectively, functional evenness and divergence. FEve and FDiv appear to be valid indices according to our criteria (Table 3). Although calculating FDiv or FEve on presence-absence data is possible, the abundance contribution to function diversity will be missing, so abundance data are always preferable for these indices. Last of all, as Q summarizes both functional richness and divergence, values should be interpreted with this in mind. Still Q is the only concave abundance-weighted estimator providing a decomposition of the quadratic entropy into alpha-, beta- and gamma-diversities (Villéger and Mouillot 2008).

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FORUM

Additive partitioning of diversity including species differences: a comment on Hardy & Senterre (2007)

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Summary

1. The distribution of biodiversity at multiple spatial scales has been traditionally investigated through the additive partitioning of γ-biodiversity (regional) into α-(within-site) and β-(among-site) components.

2. However, this decomposition is almost exclusively applied using species turnover among communities while two communities with no species in common can be very similar because they share some 'biological' similarity.

3. To overcome this limitation, Hardy & Senterre (2007) (*J. Ecol.*, **95**, 493–506) presented a new statistical framework partitioning the phylogenetic diversity into α- and β-components using the Rao's quadratic entropy.

4. We show that their decomposition is correct only when sites have the same total abundance, otherwise it may lead to negative β-diversity values. As an alternative, we provided a general decomposition of the quadratic entropy into α-, β- and γ-diversities.

5. *Synthesis.* We suggest that the 'biological' turnover quantified by the β-component of the regional quadratic entropy may help, at least, to disentangle dispersal vs. niche influences on biodiversity patterns.

Key-words: biodiversity pattern, biogeography, β-diversity, community structure, functional diversity, phylogenetic diversity, Rao's quadratic entropy

Introduction

Partitioning biological diversity within and among sites has been the focus of ecological research for several years because the pioneering works of Whittaker (1960, 1972). Indeed, the amount of species turnover among assemblages is a key component for the conservation of biodiversity and for understanding the processes underlying species distribution at multiple spatial scales. This diversity turnover was termed β-diversity while local and regional diversities were called α- and γ-diversities, respectively. In contrast to α- and γ-diversities, there is still no consensus about the measure of β-diversity because the perception of this component differs extensively among authors (Whittaker *et al.* 2001; Legendre *et al.* 2005).

Whittaker (1960, 1972) expressed β-diversity using a multiplicative model where, $\gamma = \beta \times \bar{\alpha}$, $\bar{\alpha}$ being the average α-diversity across sites. As the breakthrough paper of Lande (1996), the additive partition of diversity has rapidly emerged as a consensual framework to quantify the three components of diversity following the formula: $\gamma = \beta + \bar{\alpha}$. Hence, through additive partitioning, β-diversity has the same unit as α- and γ-diversities and is nothing more than a partial amount of the regional diversity and, as such, deserves to be properly quantified.

In most studies dealing with additive partitioning of diversity, the term β-diversity is almost exclusively applied to species turnover among assemblages. In other words, species are assumed to have the same level of 'biological' dissimilarity between each other, that is all the 'biological' distances between species pairs are the same. However, two communities can be very dissimilar in terms of species composition, with few species in common, but very similar from a phylogenetic or functional point of view. This would be the case for two assemblages with no species in common but containing the same functional groups. It is thus surprising that current measures of β-diversity ignore what makes species different in an assemblage: their relative abundances and their biological traits. This kind of species-based measure is a narrow view of β-diversity and we trust that we can obtain a completely different degree of β-diversity among assemblages if, instead of relying solely on species composition, we also take into account relationships among species, be they phylogenetic or functional.

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Analogous to the intra vs. interspecific genetic diversity distinction, Hardy & Senterre (2007) presented a new statistical framework partitioning phylogenetic diversity into α-(within-site) and a β-(among-site) components. Their measures of the diversity components are based on the Rao's quadratic entropy (Rao 1982) in the sense that they include species relative abundances and distances among species (phylogenetic distances). Here we argue that their additive partitioning of the Rao's quadratic entropy is correct only when the different sampled communities hold exactly the same total abundance, which is rarely the case in ecology. Otherwise, we show that their proposal may lead to negative β-diversity values which are not interpretable. Keeping the relevant framework of Hardy & Senterre (2007) and using the seminal contribution of Ricotta (2005), we formalize a flexible additive partitioning of diversity taking into account species differences.

The framework of Hardy & Senterre (2007)

In their paper, Hardy & Senterre (2007) proposed the following framework for diversity decomposition: let A_{ik} being the abundance (number of individuals or biomass) of species *i* within site *k*; its relative abundance within site *k*, f_{ik}, is thus $f_{ik} = A_{ik}/\sum_i A_{ik}$, and its relative abundance over all sites, $f_{i.}$, is $f_{i.} = \sum_k A_{ik}/\sum_k \sum_i A_{ik}$.

The distance between species *i* and *j* was noted δ_{ij}.

The total or regional diversity (γ), according to the quadratic entropy (Rao 1982), was defined as

$$D_T = \sum_i \sum_j \delta_{ij} f_{i.} f_{j.} \qquad \text{eqn 1}$$

The diversity within site *k* (α) was

$$D_k = \sum_i \sum_j \delta_{ij} f_{ik} f_{jk} \qquad \text{eqn 2}$$

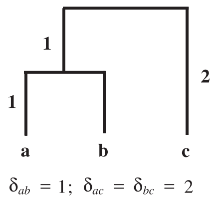
The average within-site ($\bar{\alpha}$) diversity, D_S, was presented as the expectation of D_k over all sites. The β-diversity is then the difference $D_T - D_S$ according to the additive partitioning of diversity: $\beta = \gamma - \bar{\alpha}$.

In Fig. 1 we present a case study where these formula lead to $D_S > D_T$, so to a negative β-diversity. Actually if the formulae proposed by Hardy & Senterre (2007) are correct to compute D_k and D_T based on the quadratic entropy, it is not the case for D_S. Indeed if we consider *N* sites, Hardy & Senterre (2007) calculate D_S as $D_S = (1/N)\sum_{k=1}^{N} D_k$, therefore, giving the same weight (1/*N*) to all sites without taking into account the total abundance at each site.

Consider a case with three sites, all having the same three species but where total abundances are unbalanced between sites (Fig. 1). In this example we consider that the samples from the three sites are not biased, that is, they reflect the community structure and composition of each site. The three species are placed on a theoretical phylogenetic tree and an ultrametric distance can be derived between all species pairs (Fig. 1, top right). The sites with low total abundances (sites 1 and 3) have a high α-diversity value ($D_1 = \alpha_1 = D_3 = \alpha_3 = 1.125$) whereas site 2, with the highest total abundance, has a relatively low α-diversity ($D_2 = \alpha_2 = 0.191$). Then the average α-diversity (D_S) is high (0.814) because Hardy & Senterre (2007) give the same weight to all sites regardless of their total abundance. In parallel, γ-diversity (D_T) computed using species relative abundances over all sites ($f_{i.}$) is mainly determined by the most abundant species and hence its value is lower than D_S ($D_T = 0.582 < D_S$). Finally, we obtain a negative β-diversity value $D_T - D_S = -0.232$ – an unwanted result.

Number of individuals (A_{ik})

	Sp a	Sp b	Sp c	Total
Site 1	1	1	2	**4**
Site 2	28	1	1	**30**
Site 3	1	1	2	**4**
Total	**30**	**3**	**5**	**40**



Site relative abundances (f_{ik})

	Sp a	Sp b	Sp c	Total
Site 1	0.25	0.25	0.5	**1**
Site 2	0.934	0.033	0.033	**1**
Site 3	0.25	0.25	0.5	**1**

$\alpha_1 = 1.125$
$\alpha_2 = 0.191$
$\alpha_3 = 1.125$

$D_S = 0.814$
$D'_S = 0.388$

Regional relative abundances (p_{ik})

	Sp a	Sp b	Sp c	$f_{.k}$
Site 1	0.026	0.026	0.053	**0.105**
Site 2	0.737	0.026	0.026	**0.789**
Site 3	0.026	0.026	0.053	**0.105**
$f_{i.}$	**0.789**	**0.079**	**0.132**	**1**

$D_T = 0.582$

$D_T - D_S = -0.232$

$D_T - D'_S = 0.194$

Fig. 1. Hypothetical abundances (number of individuals) for a three species regional pool and three local communities. The distances (phylogenetical or functional) between species are ultrametric and are represented on the dendrogram on the right of the table containing abundances. From local abundances (A_{ik}) we computed species relative abundances by site (f_{ik}) and then the three local diversities (α) based on the Rao's quadratic entropy index. Similarly, using regional relative abundances (p_{ik}), we computed regional diversity (D_T). When the mean local diversity is not weighted (D_S), as suggested by Hardy & Senterre (2007), it leads to a negative value of β-diversity ($D_T - D_S$). By contrast, if we use the weighted mean local diversity (D'_S) by the contribution of each site ($f_{.k}$), then $\beta = (D_T - D'_S)$ is positive, as intuitively expected under this scenario.

Fortunately, in their application, Hardy & Senterre (2007) analysed a data set where 100 individuals were sampled in each site to estimate relative abundances. Therefore, the bias we demonstrate did not affect their conclusions. However, their estimator of D_S, $\hat{D}_S = (1/N)\sum_{k\le N}\hat{D}_k$ is neither correct for a general use, nor their estimator of D_T $\hat{D}_T = (1/(N(N-1)))\sum_k\sum_{l\ne k}\sum_i\sum_j \delta_{ij} f_{ik} f_{jl}$.

Indeed, these two last estimators are correct only when (i) total abundances are equivalent among sites and samples are not biased; (ii) samples from the different sites contain exactly the same total abundance (the sampling effort would force the samples to contain the same total abundance); or (iii) total abundances across communities are purely artificial results of sampling effort and can be normalized to a predefined number of individuals.

These three cases are not the norm in ecology and if total abundances reflect real species abundances in different sites we have to use the formula provided by Ricotta (2005) and then the proposed corrections would be appropriate to estimate the correct average α-quadratic entropy and accordingly, the correct β-quadratic entropy. Indeed, Ricotta (2005) gives a weight to each site that is proportional to its relative abundance over sites ($f_{.k}$), to estimate the average α-diversity and his formula is equivalent to: $D_S' = \sum_{k=1}^{N} f_{.k} D_k$.

With: $f_{.k} = \dfrac{\sum_i A_{ik}}{\sum_k \sum_i A_{ik}}$

Using this last formula we obtained with our example an average within-site (α) diversity of $D_S' = 0.388$ and then $D_\beta = 0.194$ instead of -0.232 (Fig. 1, bottom). It means that the phylogenetic structure is dissimilar among the three assemblages, which is the case.

Additive partitioning of the Rao's quadratic entropy

Ricotta (2005) paved the way to the correct estimation of the α-, β- and γ-diversity components of Rao's quadratic entropy but Hardy & Senterre (2007) propose a complete framework with parameter estimations. Here we show that the Rao's γ-diversity can be decomposed into an intra-site and inter-site components but that those two components do not correspond to α- and β-diversities.

Our new decomposition is based on p_{ik} which is the relative abundance of species i in site k over all sites (hereafter called regional relative abundance) with:

$$p_{ik} = \frac{A_{ik}}{\sum_k \sum_i A_{ik}} = f_{ik} \times f_{.k}$$

$$f_{i.} = \sum_k p_{ik}$$

The γ-quadratic entropy (D_T) is nothing more than the sum of the distances between all pairs of species i and j within and between all pairs of sites k and l weighed by their regional relative abundances:

$$\begin{aligned} D_T &= \sum_k \sum_l \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right) = \sum_i \sum_j \delta_{ij} \sum_k p_{ik} \sum_l p_{jl} \\ &= \sum_i \sum_j \delta_{ij} f_{i.} f_{j.} \end{aligned} \qquad \text{eqn 3}$$

This is equivalent to the Formula (1) following Ricotta (2005) and Hardy & Senterre (2007).

Hence, the γ-quadratic entropy (D_T) can be divided into (i) the sum of the distances between all pairs of species i and j within sites weighed by their regional relative abundances; and (ii) the sum of the distances between all pairs of species i and j between all pairs of sites k and l ($\neq k$) weighed by their regional relative abundances. This is equivalent to an intra- vs. inter-site decomposition of the γ-quadratic entropy. More formally we obtain the additive partitioning:

$$\begin{aligned} D_T &= \sum_k \sum_l \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right) \\ &= \sum_k \sum_i \sum_j \delta_{ij} p_{ik} p_{jk} + \sum_k \sum_{l \neq k} \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right) \end{aligned} \qquad \text{eqn 4}$$

Which is equivalent to: $D_T = D_{\text{Intra}} + D_{\text{Inter}}$

In addition we have:

$$\begin{aligned} D_{\text{Intra}} &= \sum_k \sum_i \sum_j \delta_{ij} p_{ik} p_{jk} = \sum_k \sum_i \sum_j \delta_{ij} f_{ik} f_{.k} f_{jk} f_{.k} \\ &= \sum_k f_{.k}^2 \sum_i \sum_j \delta_{ij} f_{ik} f_{jk} = \sum_k f_{.k}^2 D_k \end{aligned} \qquad \text{eqn 5}$$

Then, using eqn 4, β-diversity can be expressed as:

$$\begin{aligned} D_\beta = D_T - D_S &= \sum_k \sum_i \sum_j \delta_{ij} p_{ik} p_{jk} \\ &+ \sum_k \sum_{l \neq k} \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right) - \sum_k f_{.k} D_k \end{aligned}$$

And using eqn 5 we obtained:

$$D_\beta = \sum_{k=1} f_{.k}^2 D_k + \sum_k \sum_{l \neq k} \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right) - \sum_{k=1} f_{.k} D_k$$

Finally, we can express the β-diversity as:

$$D_\beta = \sum_k (f_{.k}^2 - f_{.k}) D_k + \sum_k \sum_{l \neq k} \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right) \qquad \text{eqn 6}$$

So, as $0 \leq f_{.k} \leq 1$ and $f_k^2 - f_{.k} \leq 0$, D_β is less than the inter-site component of the quadratic entropy.

D_β is also:

$$D_\beta = \sum_k f_{.k}(f_{.k} - 1) D_k + \sum_k \sum_{l \neq k} \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right)$$

With $\sum_{l \neq k} f_{.l} = 1 - f_k$ we obtained:

$$D_\beta = -\sum_k f_{.k} \sum_{l \neq k} (f_{.l}) D_k + \sum_k \sum_{l \neq k} \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right)$$

$$D_\beta = \sum_k \sum_{l \neq k} \left(\sum_i \sum_j \delta_{ij} p_{ik} p_{jl} \right) - \sum_k \sum_{l \neq k} f_{.k} f_{.l} D_k$$

$$D_\beta = \sum_k \sum_{l \neq k} f_{.k} f_{.l} \left(\sum_i \sum_j \delta_{ij} f_{ik} f_{jl} \right) - \sum_k \sum_{l \neq k} f_{.k} f_{.l} D_k \qquad \text{eqn 7}$$

$$D_\beta = \sum_k \sum_{l \neq k} f_{.k} f_{.l} \left[\sum_i \sum_j \delta_{ij} (f_{ik} f_{jl} - f_{ik} f_{jk}) \right]$$

$$D_\beta = \sum_k \sum_{l \neq k} f_{.k} f_{.l} \left[\sum_i \sum_j \delta_{ij} f_{ik} (f_{jl} - f_{jk}) \right]$$

Using this new expression of β-diversity, it appears that D_β equals zero when all the $f_{jl} - f_{jk} = 0$, so $f_{jl} = f_{jk}$, for each species *j* and for each couple of sites (*k*, *l*). In other words, species must have the same relative abundances in each site to obtain $D_\beta = 0$.

Conclusion

We show that, despite the importance of the framework proposed by Hardy & Senterre (2007), their decomposition of the quadratic entropy into α-, β- and γ-diversities may lead to negative β-diversity values because the average α-diversity may exceed γ-diversity. Here we propose a correct decomposition of the quadratic entropy into α-, β- and γ-diversities based on the initial proposal of Ricotta (2005). In addition, we show that α- and β-diversity components do not correspond to the partition of γ-diversity into the intra-site and the inter-site components. Indeed, β-diversity is not simply the sum of the distances between all pairs of species *i* and *j* between all pairs of sites *k* and *l* ($k \neq l$) which is the inter-site component of the quadratic entropy. In a similar vein, α-diversity is not the sum of the distances between all pairs of species *i* and *j* in each site which is the intra-site component of the quadratic entropy. Instead, the α-component of the quadratic entropy is the average within-site diversity while the β-component is a 'biological' turnover across sites, which expresses the differentiation among sites using pairwise differences between species, be they phylogenetic or functional.

We suggest that β-diversity based on species 'biological' dissimilarities and species relative abundances will not react as classical β-indices based solely on species composition. Moreover, as demonstrated by Champely & Chessel (2002) and underlined by Ricotta (2005), the additive decomposition of Rao's entropy is not limited to ultrametric distances, such as, those extracted from phylogenetic trees. Rather, Euclidean distances between species pairs satisfy the same properties. As such, our additive partitioning of diversity allows the use of functional distances and a decomposition of functional diversity across scales. Because functional traits may reveal mechanisms underlying community structure (Mason *et al.* 2007; Mouillot *et al.* 2007; Petchey *et al.* 2007) we trust that the relative values of α-, β- and γ-functional diversity components will be investigated in the near future. In this perspective, we agree with Hardy & Senterre (2007) who suggest expressing β-diversity as a percentage of γ-diversity using $\beta_{st} = \beta/\gamma$ in order to compare β-diversity values between studies.

More generally, the decomposition of the quadratic entropy into α-, β- and γ-diversities has the potential to shed light on many macro-ecological patterns and may contribute to disentangling the effects of dispersal, niche filtering and competitive interactions in community establishment. For instance, even with no environmental gradient, we can expect an increase in species turnover with geographic distance because of dispersal limitation (e.g. Thompson & Townsend 2006). However, 'biological' turnover based on species' 'biological' differences may stay at a low-level if a niche process selects species composition according to their biological traits. Indeed we may expect very similar communities even between distant sites if environmental conditions are similar. Therefore, β-diversity based on the quadratic entropy quantifies a new facet of community similarity that can be useful to discriminate between niche vs. dispersal influences on biodiversity patterns.

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Chapitre 4

Bases de données utilisées

L’application écologique des travaux méthodologiques présentés dans les deux précédents chapitres a été menée sur les communautés de poissons de la lagune de Terminos. Pour cela nous avons utilisé deux types de données. Tout d’abord quatre bases de données écologiques « classiques » regroupant des données environnementales et biologiques (abondances d’espèces) acquises lors de campagnes de terrain. Parallèlement, des traits fonctionnels ont été mesurés sur les poissons collectés lors de ces campagnes.

Ces différentes bases de données sont décrites dans chacune des applications, mais je les présente ici afin de préciser certains aspects méthodologiques et surtout pour faciliter la lecture des chapitres suivants.

4.1 Données écologiques

La lagune de Terminos fait l’objet d’investigations de la part des chercheurs mexicains depuis les années 1960 et la prise de conscience de l’importance écologique de cet écosystème (cf Gomez-Aguirre 1974, Yáñez-Arancibia *et al.* 1980). De grandes campagnes d’échantillonnage ont ainsi été menées pour étudier les différents compartiments abiotiques et biotiques : hydrologie, courants, sédiments, végétation du bassin versant, végétation aquatique et necton (principalement crevettes et poissons).

Dans cette thèse, nous avons utilisé les données provenant de quatre campagnes d’échantillonnage (Tableau 4.1). Ces quatre campagnes correspondent en fait à deux programmes distincts en termes de sites d’échantillonnage et ont été regroupées en deux grandes bases de données.

4.1.1 Protocole de pêche

Le protocole d’échantillonnage du necton est identique pour les quatre campagnes d’échantillonnage. Il est fait à bord d’une petite embarcation de pêche de 7m de long (« lancha », Photo 4.2) à l’aide d’un chalut à crevettes (Photo 4.3).

Base de données	Campagne d’échantillonnage	Période	Nombre de stations	Variables environnementales	Données biologiques
Suivi long terme Lagune de Terminos	Yáñez-Arancibia	Février 1980 - Janvier 1981	17	Profondeur Transparence Salinité* Température*	Nombre d’individus et biomasse de chaque espèce de poisson
	Ramos-Miranda	Février 1998 - Janvier 1999			
Gradient environnemental Transect côte-lagune	Projet SISIERRA	Février 2003 - Janvier 2004	37	Profondeur Transparence Salinité* Température* pH* O_2 dissous*	Nombre d’individus et biomasse de chaque espèce du necton
	Projet FOMIX	Février 2006 - Janvier 2007			

Table 4.1. Résumé des deux bases de données utilisées dans cette thèse. Pour les quatre campagnes, la fréquence d’échantillonnage était mensuelle.
* paramètres mesurés en surface et au fond

Les caractéristiques du filet sont une longueur de 5m, un diamètre d’ouverture de 2,5m et un maillage de 19mm. Chaque trait est fait en ligne droite durant 12 minutes à une vitesse de 2,5 nœuds. Le volume d’eau échantillonné est donc de $4500m^3$, et correspond à une surface projetée de $2000m^2$.

Cette méthode de pêche active est la plus appropriée au cas d’étude. En effet, la très grande majorité des organismes nectoniques présents dans cet écosystème estuarien sont des juvéniles ou des adultes dont la taille maximale est inférieure à 30cm. Par conséquent les dimensions du filet et la vitesse de trait sont suffisantes pour les capturer. La seule limitation concerne les gros individus capables de nager assez vite pour ne pas être capturés. Cependant, durant l’échantillonnage plusieurs gros individus appartenant à des espèces a priori rapides ont été capturés, par exemple deux raies de plus de 2kg (*Gymnura micrura* et *Rhinoptera bonasus*) et un *Lobotes surinamiensis* de 1,4kg.

Photo 4.2. Bateau utilisé pour l’échantillonnage. Longueur : 6m, puissance du moteur 50ch.

Photo 4.3. Chalut utilisé pour l’échantillonnage du necton

Par ailleurs, ce type de chalut permet de collecter les organismes à la fois près du sédiment et dans la colonne d’eau, qui est relativement peu profonde (3,5m en moyenne). Ainsi, nous observons dans les pêches des espèces typiquement benthiques (poissons plats, raies pastenagues) et d’autres typiquement pélagiques (anchois).

Les individus pêchés sont stockés dans la glace sur le bateau avant d’être congelés au laboratoire afin d’être conservés jusqu’à leur analyse. Tous les individus péchés ont été identifiés à l’aide des clés de Cervigón *et al.* (1992); Fischer (1978); Castro-Aguirre (1978); Reséndez (1981a); Reséndez (1981b) et Aguirre-León & Yáñez-Arancibia (1986) ; puis pesés au décigramme près.

4.1.2 Campagnes d'échantillonnage

La première base de données correspond à deux campagnes conduites à l'intérieure de la lagune à 18 ans d'intervalle. Elle regroupe les données récoltées en 1980-81 par Alejandro Yáñez-Arancibia (Yáñez-Arancibia *et al.* 1982) et celles issues de l'échantillonnage mené par Julia Ramos-Miranda (Ramos-Miranda 2000) en 1997-1999.

Yáñez-Arancibia et collaborateurs ont échantillonné mensuellement 18 stations de février 1980 à avril 1981. Ramos-Miranda et collaborateurs ont pour leur part mené un suivi mensuel sur 23 stations d'octobre 1997 à mars 1999. Pour ces deux campagnes d'échantillonnage, le suivi concernait à la fois les paramètres hydrologiques et les communautés nectoniques. Les variables environnementales relevées sont : la profondeur, la transparence (mesurée avec un disque de Secchi), la salinité et la température (Table 4.1).

Parmi les 18 stations définies par Yáñez-Arancibia, 17 sont très proches géographiquement de celles échantillonnées par Ramos-Miranda, et ont donc été retenues pour la comparaison entre les deux périodes (Figure 4.4).

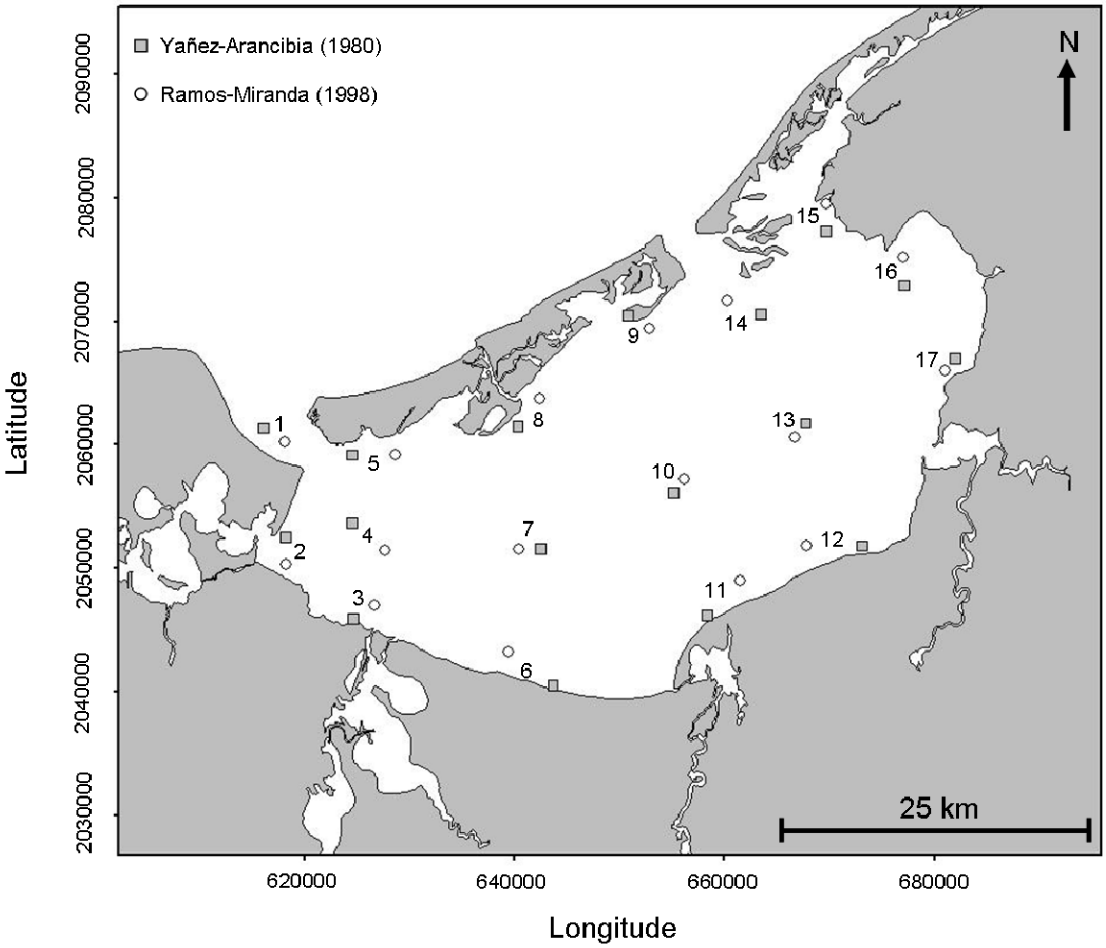

Figure 4.4. Carte des échantillonnages menés sur la lagune de Terminos en 1980 et 1998

De manière similaire, seules les données de 12 mois consécutifs ont été retenues pour les analyses, soit respectivement pour les deux campagnes, du mois de février 1980 à janvier 1981 et du mois de février 1998 au mois de janvier 1999.

La base de données finale contient donc les données environnementales et biologiques (nombre d'individus et biomasse de chaque espèce de poisson) relevées, mensuellement durant un an dans 17 stations à 18 ans d'intervalle, soit au total 2x12x17=408 points de relevés. Cette large base de données est donc adaptée à l'analyse des changements temporels survenus dans la lagune de Terminos.

La seconde base de données est plus récente et regroupe deux campagnes identiques menées à 3 ans d'écart. Le site d'étude est plus vaste et s'étend de la partie sud-ouest de la lagune de Terminos à l'embouchure du Rio Usumacinta (Figure 4.5). Cette zone est à la fois influencée par les décharges des trois fleuves adjacents et par les entrées marines notamment au nord de l'île de Carmen. Elle est par conséquent caractérisée par une très forte hétérogénéité des conditions environnementales (profondeur, salinité, transparence, courant).
Ce transect de 150 km de long est ponctué de 37 stations localisées par GPS (précision 5m). Ces stations ont été échantillonnées mensuellement durant 12 mois, respectivement entre février 2003 et janvier 2004 et entre février 2006 et janvier 2007. Les variables environnementales relevées étaient la profondeur, la transparence (mesurée avec un disque de Secchi), et la température, la salinité, le pH et la quantité d'oxygène dissous mesurés à l'aide d'une sonde (Hydrolab HL 2011) en surface et près du fond.

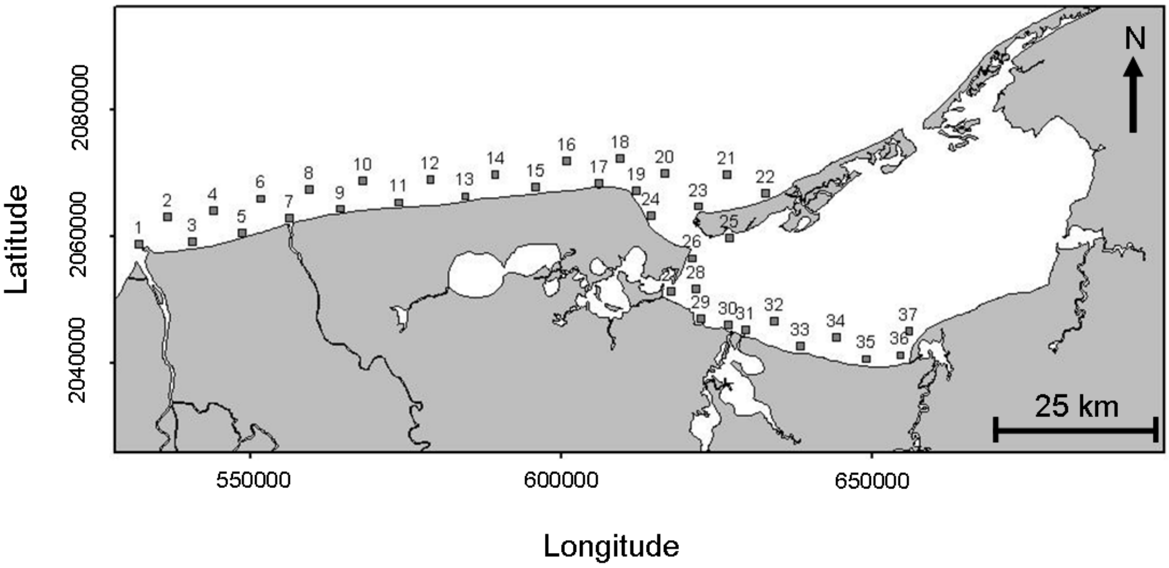

Figure 4.5. Carte du transect côtier échantillonné en 2003 et en 2006

Le protocole de pêche était celui décrit précédemment, à la différence près que tous les organismes nectoniques, et non plus seulement les poissons, ont été identifiés et pesés. Ceci inclut, les crevettes (famille Penaeidae), les crevettes mantes (fam. Squillidae), les crabes (fam. Portunidae), les calamars (fam. Janiroidae), les raies (fam. Rajidae et Myliobatidae) et les poissons téléostéens.

Au final, cette base de données contient les données environnementales et écologiques pour 2 périodes x 12 mois x 37 stations = 888 points d‘études. Elle couvre une courte période mais, du fait de la répartition des points d’échantillonnage, elle couvre un très fort gradient environnemental.

4.1.3 Bilan des quatre campagnes

Au total les deux bases de données contiennent 133 espèces de poissons avec 9 espèces de chondrichtyens représentant 3 ordres et 124 téléostéens appartenant à 14 ordres (Annexe A). Dans chacune des bases la richesse spécifique est autour de 80 espèces (de 77 à 89). Cette forte diversité taxinomique est caractéristique des milieux estuariens tropicaux (Blaber 2002). Elle s’accompagne notamment d’un fort turnover entre les différentes communautés, en relation avec la forte variabilité des conditions environnementales.

La biomasse totale péchée va de 286 à 557kg et le nombre d’individus de 10 000 à 46 000 (Table 4.6).

						Espèces fonctionnellement caractérisées		
Base de données	Campagne	Période	Nombre d'espèces	Biomasse (kg)	Nombre d'individus	Nombre	% biomasse	% individus
Suivi long terme Lagune de Terminos	Yáñez-Arancibia	1980 - 1981	77	429	10 637	53	98,99	98,22
	Ramos-Miranda	1998 - 1999	89	286	12 197	58	98,41	98,88
Gradient environnemental Transect côte-lagune	Projet SISIERRA	2003 - 2004	87	557	46 012	63	99,28	99,36
	Projet FOMIX	2006 - 2007	87	398	25 639	70	99,73	99,88

Table 4.6. Synthèse des données écologiques pour les quatre bases de données utilisées.

4.2 Traits fonctionnels

Afin de décrire fonctionnellement les espèces de poissons présentes dans la région étudiée, nous avons retenu deux fonctions biologiques majeures : l'acquisition des ressources alimentaires et la locomotion. Au cours des analyses (Manuscrits F et H), ces deux fonctions ont été traitées indépendamment. Je présente ici le protocole de mesure de ces traits morpho-anatomiques, en me focalisant plus particulièrement sur les aspects méthodologiques et techniques mis en oeuvre, sans reprendre les idées et concepts présentés dans le Manuscrit A.

4.2.1 Collecte des individus

Les individus sur lesquels les traits ont été mesurés proviennent de la campagne 2006-2007. Comme expliqué précédemment, une fois capturés au chalut tous les individus étaient conservés dans la glace sur le bateau puis congelés au laboratoire pour être conservés jusqu'aux phases d'identification et de mesures.

Après identification, j'ai sélectionné certains individus sur lesquels mesurer les traits. L'objectif initial était de mesurer les traits sur le plus grand nombre d'espèces possible, en se limitant à 20 individus par espèce. Ces individus ont donc été collectés au cours des 12 mois de l'étude et en provenance de différentes stations. Ce choix relativement aléatoire était toutefois dicté par deux critères pour les espèces suffisamment abondantes : les individus devaient être en bon état physique (intégrité des nageoires notamment) et leur taille devait être représentative de la taille moyenne observée dans l'espèce. Cette gamme de taille moyenne avait été estimée au préalable sur les bases de données antérieures.

4.2.2 Mesures morphologiques[1]

La largeur maximale du corps (*Bw*), la hauteur (*Md*) et la largeur maximales de la bouche (*Mw*) ont été réalisées à l'aide d'un pied à coulisse électronique avec une précision de 0,1mm. Pour cela, la bouche était ouverte au maximum sans toutefois faire jouer l'éventuelle élasticité de la mâchoire ou de la protrusion.

Le poisson était alors étendu sur un repère quadrillé (pas de 5mm), le profil gauche visible avec la nageoire pectorale gauche et la nageoire caudale étalées (Figure 4.7).

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[1] les abréviations utilisées sont en anglais par cohérence avec les manuscrits

Les prises de vue ont été effectuées à l’aide d’un appareil photo numérique (Canon PowerShot G6, résolution 7 millions de pixels, compression jpeg minimale), placé verticalement à au moins 20 cm de distance pour limiter les distorsions. Au total, trois photos ont été prises pour chaque individu, une du poisson entier (**E**), une de la partie antérieure (**A**), du museau à l’arrière de la nageoire pectorale, et une de la partie postérieure (**P**), de la nageoire anale à la nageoire caudale (Figure 4.7).

Les mesures morphologiques ont été réalisées à l’aide du logiciel *ImageJ* avec une précision au 1/10ème de millimètre (cf encadré sur les erreurs de mesure).

Erreurs de mesure liées à l’analyse d’image

Des tests préalables sur des mires ont montré que l’erreur totale pour les mesures faites sur les photos était de l’ordre de 2% (données personnelles). Les facteurs d’erreur sont les distorsions de l’image dues à l’objectif de l’appareil photo et à l’éventuelle non orthogonalité entre l’axe de la photo et le plan du poisson, et l’erreur de mesure lors du pointage des extrémités du segment sous ImageJ.

Néanmoins, cette erreur de 2% reste relativement faible et est sans doute largement inférieure à celle obtenue avec un pied à coulisse. En effet, il est très difficile de mesurer avec une grande précision une longueur sur un objet humide et mou telle une nageoire. Par ailleurs, l’analyse d’image permet de mesurer des surfaces de manière fiable et très rapide.

Sur la photo du poisson en entier (Figure 4.7 E), deux mesures sont réalisées :

- la *longueur standard* (*Bl*) mesurée sur le segment allant de l’extrémité du museau à la base de la nageoire caudale[1]
- la *hauteur maximale du corps* (*Bd*), souvent située à la verticale de l’insertion de la nageoire pectorale

Sur la photo de la partie postérieure du corps (Figure 4.7 P), trois mesures sont faites :

- la *hauteur minimale du pédoncule caudal* (*CPd*)
- la *hauteur maximale de la nageoire caudale* (*CFd*)
- la *surface de la nageoire caudale* (*CFs*)

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[1] mais cf la revue de Howe (2002) sur le caractère parfaitement non standardisé de la notion de longueur standard en ichtyologie

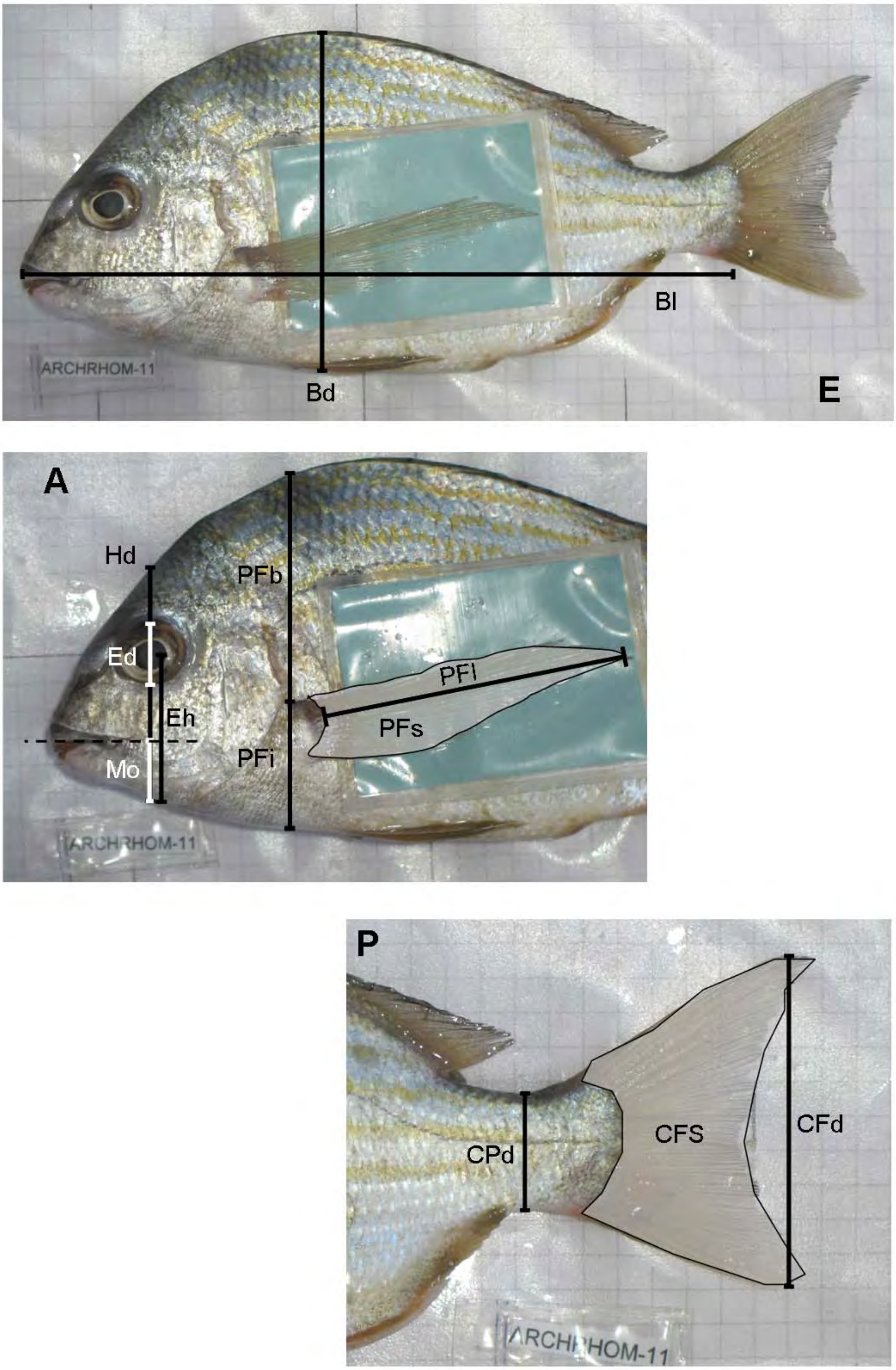

Figure 4.7. Exemples de photos utilisées pour les mesures morphologiques. Les longueurs sont figurées par les segments noirs et les surface sont grisées. Voir le texte pour la liste des mesures.

Sur la photo de la partie antérieure du corps (Figure 4.7 A), huit mesures sont réalisées :

- la *longueur maximale de la nageoire pectorale* (*PFl*)
- la *surface de la nageoire pectorale* (*PFs*)
- la *hauteur du corps à la verticale de l'insertion de la nageoire pectorale* (*PFb*), en pratique souvent confondue avec *Bd*
- la *hauteur entre la base inférieure du corps et le point supérieur d'insertion de la nageoire pectorale* (*PFi*), qui est donc une section de *PFb*
- le *diamètre maximum de l'œil* (*Ed*), pris verticalement
- la *hauteur de la tête dans l'axe de l'œil* (*Hd*)
- la *hauteur entre le centre de l'œil et la base inférieure du corps* (*Eh*), qui est donc une section de *Hd*
- la *hauteur entre l'extrémité avant de la mâchoire supérieure et la base inférieure du corps* (*Mo*), qui est donc une section de *Hd*

4.2.3 Mesures anatomiques

Après ces prises de vues, l'opercule gauche était enlevée et la branchie la plus externe prélevée. La longueur (au $1/10^{\text{ème}}$ de mm) de la plus longue branchiospine (*GRl*) était alors mesurée à l'aide d'un micromètre oculaire sous une loupe binoculaire

Finalement, la cavité générale était ouverte et l'appareil digestif, de l'œsophage à l'anus, extrait. Il était alors étalé, en particulier les replis intestinaux au niveau du pancréas diffus, et sa longueur totale mesurée à 5mm près (*Gl*).

4.2.4 Traits fonctionnels dérivés des mesures morpho-anatomiques

Comme expliqué précédemment, les espèces ont été caractérisées fonctionnellement pour l'acquisition des ressources et la locomotion. Ces deux fonctions sont complexes et font intervenir plusieurs organes. Elles ne peuvent donc pas être décrites avec seulement un ou deux traits. J'ai donc retenu respectivement 7 et 10 traits morpho-anatomiques pour les décrire. Ces traits fonctionnels sont calculés à partir des 19 mesures morpho-anatomiques présentées ci-dessus.

La masse (transformée logarithmiquement) est commune aux deux fonctions et quantifie la taille de l'animal. Les 15 autres traits fonctionnels sont des ratios entre des mesures morpho-anatomiques et quantifie les formes ou la taille relative des organes.

Pour l'acquisition de la nourriture la bouche est décrite par sa forme (*Osh*), sa surface relative par rapport à la section du corps (*Osf*), et sa position verticale sur la tête (*Ops*). L'œil (*Edst*), et les branchiospines sont décrits par leur taille relative par rapport à la hauteur de la tête (*GRlst*). Enfin, la longueur du tube digestif (*Glst*) est comparée à la longueur standard du corps.

Pour la locomotion, les traits fonctionnels regroupent, la position verticale de l'œil sur la tête (*Eps*), la forme (*Bsh)* et la surface relative *(Bsf)* de la section du corps ; la position verticale *(PFps)* et la forme *(PFar)* de la nageoire pectorale ; l'étranglement du pédoncule caudal *(CPt)*, la forme de la nageoire caudale *(CFd)* et enfin le ratio entre les surfaces des nageoires pectorales et caudale *(Frt)* et leur surface totale comparée à la section du corps *(Fsf)*.

4.2.5 Cas particuliers

De nombreuses espèces de poissons ont des morphologies très éloignées de la forme classique d'un perciforme type (exemple : poisson rouge *Carassius auratus*). Ceci nécessite d'utiliser des conventions pour les mesures morphologiques et les valeurs de traits fonctionnels qui en découlent. Je ne redétaillerai pas ici les idées développées dans le Manuscrit A, mais je vais juste préciser les points importants concernant le protocole que j'ai mis en pratique sur les espèces de la lagune de Terminos.

Absence d'organes

Certains poissons n'ont pas de nageoire caudale (ex: Anguilliformes). Il est alors impossible de mesurer la hauteur et la surface de la nageoire caudale. Par conséquent, la valeur des deux traits fonctionnels (*CFar* et *Frt)* concernés par la morphométrie de la nageoire caudale a été fixée à 0.

Cas des raies (Rajiformes et Myliobatiformes)

En faisant abstraction de leur squelette cartilagineux, les raies peuvent être assimilées fonctionnellement à des téléostéens fortement aplatis verticalement (comme certaines espèces d'Ogocephalidae). Les mesures morphologiques sont donc inchangées. En revanche les photos ne peuvent être prises que vue de dessus et par conséquent toutes les mesures faites sur le profil doivent être réalisées au pied à coulisse. Néanmoins, certaines mesures anatomiques peuvent être fixées par convention. Ainsi, lorsque la bouche est en face ventrale (comme chez les Rajiformes), la position de la bouche (*Ops)* peut directement être fixée à 0. De même chez les Rajiformes la position de l'œil *Eps* sur le dessus de la tête est caractérisée par la valeur 1. Les surfaces des nageoires pectorales et caudales sont mesurables sur les photos vues de dessus.

Cas des Pleuronectiformes

Les poissons plats présentent une morphologie très particulière avec d'une part des caractères anatomiques de téléostéens (squelette, mouvements des nageoires), mais d'autre part du fait de la latéralisation, ils sont fonctionnellement plus proches des raies ou des poissons aplatis verticalement. Cette dichotomie implique certaines conventions lors de l'application des mesures morpho-anatomiques puis des traits fonctionnels (cf Manuscrit A).

Les photos ont été prises sur la face colorée. Fonctionnellement, cette face constitue le haut du corps de l'animal lorsqu'il repose sur le substrat. Par conséquent, la largeur du corps correspond ici à la distance maximale entre les nageoires dorsale et anale. A l'inverse, la hauteur est mesurée au pied à coulisse entre les deux nageoires pectorales. La forme du corps des poissons plats (*Bsh*) est donc caractérisée par une valeur très faible, similaire à celle des raies.

Par contre, même si le mouvement de la nageoire caudale suit une orientation verticale dans le milieu de vie, il reste déterminé par l'organisation du squelette et des muscles du pédoncule caudal. Par conséquent tous les traits mesurés sur la nageoire caudale sont fait sur l'image de la partie postérieure du poisson en faisant abstraction de la latéralisation.

Les nageoires pectorales, au sens fonctionnel de nageoires perpendiculaires à l'axe du corps, sont pour les poissons plats les nageoires dorsale et anale. Leur rôle a été considéré comme négligeable et les traits *PFps* et *PFar* ont été fixés à une valeur nulle.

4.2.6 Nombres d'individus et d'espèces caractérisées

Au cours de la campagne d'échantillonnage 2006-2007, les traits ont été mesurés sur 1031 individus appartenant à 70 espèces (Table 4.8). Par ailleurs, comme aucun *Lutjanus griseus*, espèce relativement abondante dans les bases de données 1980-1998, n'avait été pêché au cours des 12 missions, j'ai eu recours au marché local pour en obtenir 10 individus. Au final sur ces 71 espèces, 40 sont caractérisées fonctionnellement à partir de 20 individus et

55 avec plus de 5 individus (Table 4.8). Seules 6 espèces ne sont représentées que par 2 individus.

Nombre d'individus mesurés	Nombre d'espèces
2-5	16
6-10	9
11-15	4
16-20	42
TOTAL	**71**

Table 4.8. Distribution des tailles d'échantillons.

Les espèces fonctionnellement caractérisées contribuent dans toutes les bases de données à plus de 98% de la biomasse et du nombre d'individus collectés (Table 4.6). En effet, les espèces non caractérisées sont pour la plupart représentées par moins de 10 individus et contribuent donc très marginalement aux abondances des communautés.

4.3 Traitement des données

4.3.1 Valeur moyenne par espèce

Pour les espèces relativement rares (*i.e.* moins de 20 individus pêchés sur toute la campagne 2006-2007) certains individus avaient des organes abîmés (notamment les nageoires et le tube digestif). Par conséquent, en se fondant sur une analyse des quartiles, certaines valeurs de traits fonctionnels aberrantes ont été supprimées.

Pour chaque espèce, la valeur moyenne de chaque trait a alors été calculée sur tous les individus et seules ces valeurs moyennes ont ensuite été utilisées (Manuscrits F et G). Cette utilisation de la seule valeur moyenne suppose que la variabilité intraspécifique est globalement négligeable devant la variabilité interspécifique. Cette hypothèse semble évidente lorsque l'on considère des espèces taxinomiquement et donc très souvent morphologiquement éloignées (par exemple : un tétrodon et un sciénidé).

Cette différence peut devenir plus ténue entre certaines espèces congénériques qui parfois ne se distinguent les unes des autres que par des caractères marginaux d'un point de vue fonctionnel. Par exemple, le critère d'identification entre *Cynoscion arenarius* et *Cynoscion nothus* est le nombre de rayons de la nageoire anale qui est de 11 pour le premier et 9 pour le second. Par conséquent, le fait que certaines espèces soient très proches morphologiquement n'est pas un problème méthodologique mais au contraire souligne l'intérêt de l'approche fonctionnelle qui permet de quantifier la similarité entre espèces.

De même, les valeurs moyennes obtenues sur les individus pêchés en 2006-2007 ont été utilisées pour caractériser les communautés en 1980 et 1998 en faisant l'hypothèse que les variations morphologiques temporelles sont minimales.

Ces hypothèses résultent du fait qu'il faut trouver un compromis entre la pertinence des données et leur coût d'acquisition (de l'ordre de 20 minutes au total par individu). Certains auteurs ne mesurent les traits que sur trois individus (Bellwood *et al.* 2006b) tandis que d'autres les estiment pour plusieurs dizaines (Ibanez *et al.* 2007).

4.3.2 Le cas particulier de la masse

Il est à souligner que pour avoir une meilleure estimation, la masse moyenne des espèces n'a pas été calculée sur les quelques individus sélectionnés pour la mesure des traits fonctionnels, mais sur l'ensemble des individus présents dans les bases de données utilisées dans chaque étude. En effet, comme chaque individu est pesé il est aisé de calculer la masse moyenne de chaque espèce. Cette méthode suppose que les valeurs des autres traits fonctionnels ne changent pas en fonction de la masse. Cette hypothèse, non testée, semble acceptable compte tenu de la faible gamme de taille présente pour chaque espèce.

4.3.3 Utilisation des abondances

Pour les calculs des indices de diversité (Manuscrit F et H), seules les abondances des espèces fonctionnellement caractérisées ont été prises en compte. En effet, les espèces sur lesquelles les traits n'ont pas été mesurés ne sont présentes que très ponctuellement et lorsqu'elles sont présentes elles contribuent peu à l'abondance totale des communautés. D'un point de vue fonctionnel elles peuvent donc être négligées. Néanmoins, dans le Manuscrit F, les quelques communautés dans lesquelles moins de 80% de la biomasse appartenait aux espèces caractérisées fonctionnellement n'ont pas été incluses dans les calculs.

Chapitre 5

Stabilité spatio-temporelle de la structure fonctionnelle des communautés

5.1 Les estuaires : des écosystèmes à forte hétérogénéité environnementale qui force les remplacements d'espèces

Les écosystèmes estuariens sont caractérisés par une forte hétérogénéité environnementale, à la fois pour les variables physico-chimiques (salinité, profondeur) et les habitats (végétation, sédiment) (Blaber 2002). Ceci est à relier aux influences fluctuantes et conjointes des apports du bassin versant et de la mer. Cette forte variabilité influence les espèces qui peuplent ces écosystèmes estuariens et structure les « patrons » de biodiversité (Sosa-López *et al.* 2007). En effet, parmi toutes les espèces présentes à l'échelle régionale, seule une partie passe à travers les filtres abiotiques et biotiques et sont présentes localement (Lortie *et al.* 2004). Par exemple, la plupart des espèces ne peuvent pas tolérer toute l'étendue de la gamme de salinité présente (Sosa-López *et al.* 2007). D'autres ne pourront subsister que dans les zones où elles trouvent leurs ressources trophiques. Ainsi, la plupart des espèces ne sont présentes que dans certaines portions de l'écosystème ou durant certaines saisons. Par conséquent, il existe un fort remplacement des espèces à la fois dans l'espace (les différentes niches environnementales ou habitats de la lagune) et dans le temps (les différentes saisons).

5.2 Diversité β taxinomique versus diversité β fonctionnelle

La composition des communautés estuariennes est donc très variable et se traduit en pratique par une forte diversité β, définie comme la part de biodiversité non partagée par plusieurs communautés. Néanmoins, cette diversité β ne prend généralement en compte que les données taxinomiques. Or, considérons le cas hypothétique de deux communautés ne partageant aucune espèce et ayant donc une forte diversité β (Figure 5.1). Ces deux communautés peuvent avoir des espèces très différentes en terme d'attributs biologiques (Cas 1) mais il est aussi possible d'avoir deux communautés ayant des espèces très similaires (Cas 2). Par conséquent, une forte diversité β taxinomique peut être associée à une forte (Cas 1) ou une faible (Cas 2) diversité β fonctionnelle, définie comme la part de diversité fonctionnelle non partagée par plusieurs communautés (ici 2).

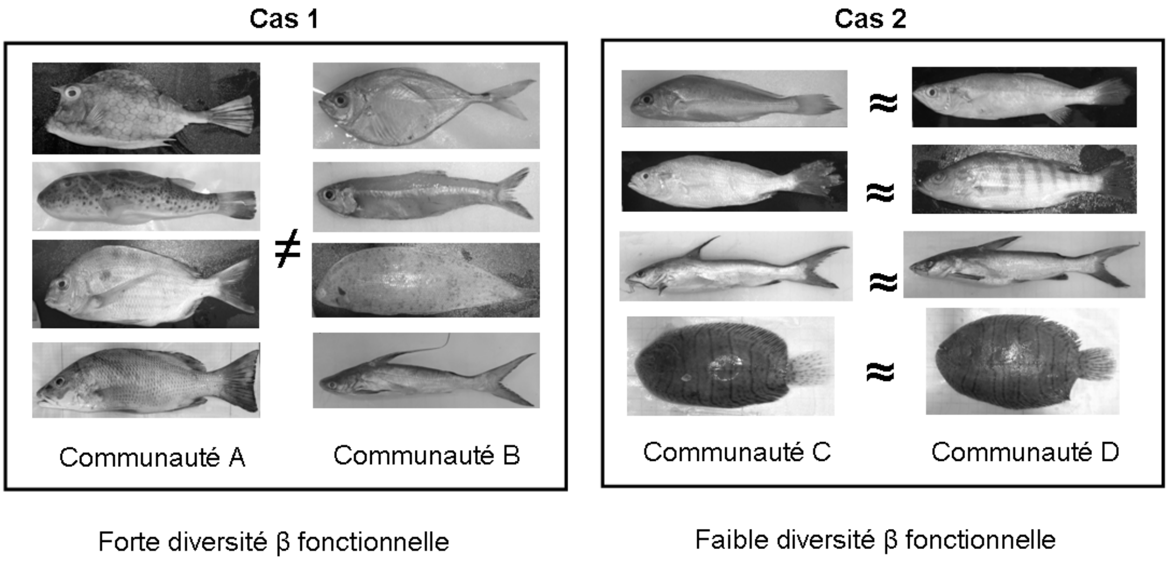

Figure 5.1. Illustration de la notion de diversité β fonctionnelle. Dans les deux cas, les communautés ne partagent aucune espèce

Il est par contre évident qu'une faible diversité β taxinomique induit forcément une faible diversité β fonctionnelle puisque les communautés partagent les mêmes espèces. Notons toutefois que dans le cas d'une forte variabilité phénotypique des traits fonctionnels (exemple : plantes poussant sur deux types de substrats), il est possible d'avoir une forte diversité β fonctionnelle malgré une diversité β taxinomique nulle.

Comme la diversité fonctionnelle influence les processus écosystémiques, il est donc primordial de quantifier ses variations dans un écosystème très hétérogène. En d'autres termes, face à la très forte variabilité dans la composition taxinomique des communautés, nous nous sommes demandé s'il existait une forte variabilité de la structure fonctionnelle des communautés de la lagune de Terminos. Nous avons donc mené deux études complémentaires, l'une sur les poissons en utilisant des traits écomorphologiques et l'autre sur le necton en considérant la structure trophique (Figure 5.2).

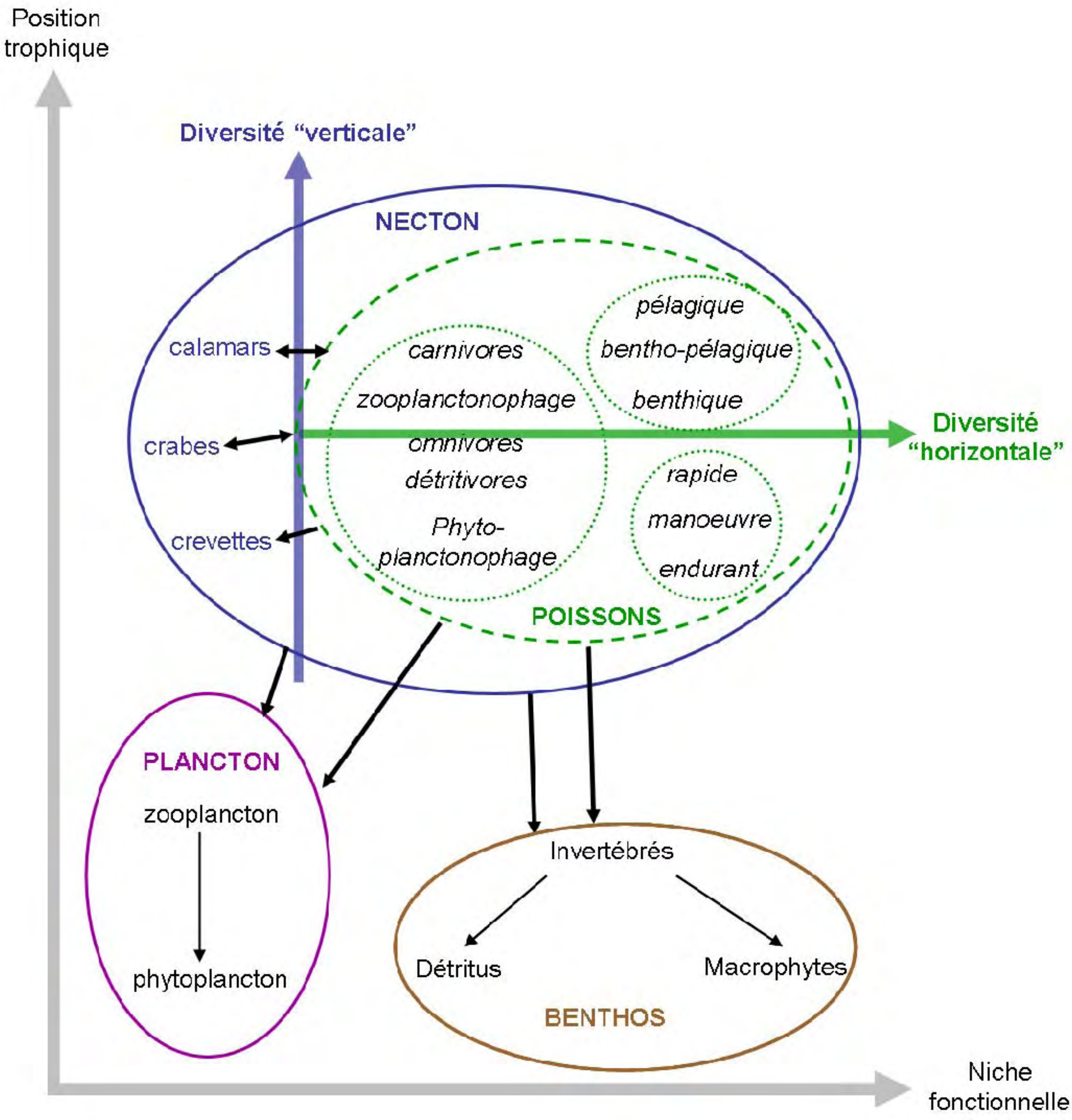

Figure 5.2. Schéma simplifié des interactions trophiques dans un écosystème aquatique, entre le necton, le benthos et le plancton. Les deux axes d'étude présentés dans ce chapitre sont symbolisés par les flèches bleue et verte. La première est parallèle à l'axe trophique et vise à caractériser la structure verticale (= trophique) du necton. Le second axe (en vert) correspond à la diversité « horizontale », c'est à dire à la diversité des stratégies fonctionnelles à l'intérieur d'un groupe trophique, ici les poissons. Elle est estimée via des traits écomorphologiques caractérisant les fonctions d'acquisition de la nourriture, de locomotion et de position dans la colonne d'eau. Des stéréotypes pour ces trois fonctions sont donnés dans les groupes en pointillés.

5.3 Stabilité dans la structure fonctionnelle des peuplements de poissons malgré l’hétérogénéité environnementale

Nous avons tout d’abord testé cette hypothèse sur les communautés de poissons (Manuscrit F, Villéger *et al.*, soumis à *American Naturalist*). Pour cela nous avons utilisé les données issues des campagnes le long du transect côtier. Ces deux bases de données présentent le double avantage de contenir un grand nombre de points d’échantillonnage (888) couvrant des conditions environnementales très variées. Nous avons considéré la variabilité spatiale (le long du transect pour un mois donné) et temporelle (au cours de l’année pour une station donnée). La diversité β fonctionnelle a été estimée suivant la méthode décrite dans le Manuscrit E et ce pour deux fonctions d’intérêt chez les poissons : l’acquisition de la nourriture et la locomotion.

Comme attendu, nous avons trouvé une forte dissimilarité dans la composition taxinomique des communautés mais par contre une faible diversité β fonctionnelle pour les deux fonctions et pour les deux échelles. Ces faibles valeurs ont été testées contre un modèle nul approprié. Ces comparaisons ont permis d’aller plus loin et de démontrer que ces valeurs de diversité β fonctionnelle étaient plus faibles que celle attendues par chance (traits aléatoirement distribués aux espèces).

Des analyses complémentaires ont aussi mis en évidence le rôle clé de deux groupes fonctionnels dans la stabilisation de la structure fonctionnelle. Ces deux groupes sont constitués d’espèces dominantes fonctionnellement proches et qui se remplacent les unes les autres le long du gradient environnemental. Plus généralement, ces résultats suggèrent que la variabilité des paramètres abiotiques induit un fort remplacement des espèces entre les différentes communautés. Néanmoins, ce remplacement n’est pas aléatoire mais se fait de préférence à l’intérieur de groupes fonctionnels dominants. Ces deux groupes contiennent respectivement des poissons chats omnivores plutôt benthiques et des sciénidés pélagiques se nourrissant d’invertébrés. Ces deux stratégies fonctionnelles semblent donc être les plus favorisées dans cet écosystème estuarien caractérisé par une faible profondeur et des dépôts important de matière organique.

5.4 Stabilité dans la structure trophique du necton malgré l'hétérogénéité environnementale

Une fois mis en évidence cette stabilité de la structure fonctionnelle des communautés de poissons, il nous a semblé nécessaire d'élargir le champ d'investigation et de considérer le necton dans son ensemble (Manuscrit G, Villéger *et al.* 2008). Pour cela, nous n'avons pas pu utiliser de traits morpho-anatomiques, du fait de la trop grande disparité des plans d'organisation des organismes étudiés (crevettes, calamars, crabes, poissons). Nous avons donc considéré le niveau trophique moyen de chaque espèce. Cet indice largement utilisé en écologie des pêcheries (Pauly *et al.* 1998) renseigne sur la position de l'espèce dans la chaîne trophique et peut être vu comme un trait fonctionnel. La diversité trophique des communautés nectoniques a ainsi pu être calculée grâce aux indices préconisés par Mason *et al.* (2005) pour les cas d'études avec un seul trait fonctionnel.

Nous avons tout d'abord testé si les composantes de la diversité trophique étaient affectées par les variables environnementales. Les résultats démontrent que malgré leur très grande variabilité spatio-temporelle, elles n'ont en réalité qu'un très faible effet sur la diversité trophique. Celle-ci est en effet très stable, avec un pic d'abondance pour les niveaux trophiques intermédiaires. Par ailleurs, cette domination est due à plusieurs espèces taxinomiquement très différentes suivant les zones et les saisons. Ce remplacement fait en particulier intervenir à la fois des poissons (principalement des sciénidés et des poissons chats) et des crabes. Ces résultats soulignent donc la pertinence de l'approche fonctionnelle, indépendante de la taxinomie, pour caractériser la structure trophique des communautés nectoniques.

Plus généralement, les conclusions tirées de l'étude sur les seuls poissons sont étayées par cette approche sur le necton. En effet, une fois encore, la forte disparité dans la composition des communautés ne se retrouve pas dans la structure fonctionnelle, ici en l'occurrence trophique. Par ailleurs, dans ce cas d'étude, nous avons testé explicitement l'effet des variables environnementales et il est clair qu'elles n'influencent pas la structure trophique, même à très petite échelle. D'un point de vue écologique, il semble donc que la structure trophique est plutôt influencée par les ressources qui sont ici abondantes du fait des apports fluviaux continus. La chaîne trophique n'est donc pas influencée par une limitation de la productivité primaire (effet de type « bottom-up »). Par ailleurs, même si la pêche n’est pas négligeable dans la zone, elle n’induit probablement pas de « top-down » puisqu’elle cible les crevettes et occasionne, du fait de la non sélectivité des chaluts à mailles très fines, une grande part de prises accessoires. Il semblerait donc que la structure trophique du necton se stabilise autour des niveaux trophiques intermédiaires, occupés principalement par des espèces omnivores.

MANUSCRIT F

Core functional groups maintain low functional β-diversity despite high taxonomic β-diversity

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Abstract

The concept of β-diversity, defined as species turnover among communities, has been widely used to investigate biodiversity patterns and community assembly rules. We develop a new aspect of β-diversity focusing on functional relationships among species rather than taxonomic diversity itself. To measure functional turnover among communities we used an additive decomposition based on the Rao's quadratic entropy index. We apply this new framework using a large dataset of estuarine fish communities at Terminos Lagoon in the south of the Gulf of Mexico. Despite high taxonomic turnover, we found a low functional β-diversity which moreover was lower than expected by chance. We explain this result by the dominance of core functional groups which maintain a low functional β-diversity among communities over space and time whatever their species composition. Our results suggest that low spatial and temporal functional turnovers observed among fish communities were due to non random associations between functional identities and abundances at the metacommunity scale, i.e. that some sets of trait values are more likely to be associated with the highest abundances, whatever the environmental conditions, the station and the season. Functional β-diversity has the potential to link metacommunity dynamics to fundamental properties such as ecosystem functioning.

Keywords: β-diversity, functional diversity, Rao's quadratic entropy, fish, estuarine ecosystem, metacommunities

Introduction

Partitioning biological diversity within and among sites has been the focus of ecological research for several decades since the pioneering works of Whittaker (1960, 1972). The biodiversity turnover among sites was early coined β-diversity while local and regional diversities were called α and γ-diversities, respectively (Whittaker 1960). The amount of β-diversity among sites is a key component for the conservation of biodiversity. Indeed, McKnight et al. (2007) identified areas of high β-diversity for amphibian, bird, and mammal taxa at a global scale which deserve particular attention since these areas are likely to be vulnerable to climate change. Measuring whether communities share similar species is also crucial for understanding the driving forces underlying community structure and composition at multiple spatial scales. For instance, Cottenie (2005) proposed a new method whereby the total variation in species composition among communities accounted for by spatial and environmental variables could be used to infer alternative models of metacommunity structure (Leibold et al. 2004).

In studies investigating diversity partitioning among communities, biodiversity is almost exclusively assimilated to species composition while the definition of biodiversity includes various facets of the diversity of life (Purvis and Hector 2000). Most current measures of β-diversity ignore what makes communities different over space and time: species relative abundances and species biological traits (but see Pavoine et al. (2004) and Ricotta (2005)). Indeed, for most of β-diversity indices, the maximum value is reached when the communities have no species in common (Koleff et al. 2003). This kind of species-based approach is an incomplete view of community structure. Indeed, two communities can be very similar from a biological point of view (biological attributes in common) but very dissimilar in terms of species composition. In other words, should a set of communities with no species in common be always assigned the lowest possible β-diversity value? The negative answer to this question raises two overlooked issues. What is the level of biological turnover among communities when environmental conditions, and thus species compositions, are highly variable? What can we learn from the examination of β-diversity values including biological and abundance differences among species?

Although seeking ubiquitous ecological structure in communities with distinct species compositions has been investigated for several decades (e.g. Winemiller 1991; Ben-Moshe et al. 2001; Irz et al. 2007), the potential of functional traits to reveal processes structuring communities has been recently emphasized (McGill et al. 2006; Ackerly and Cornwell 2007; Mason et al. 2007). A lack of significant variation in the functional structure of communities over space and time would support the existence of consistent processes shaping communities (Norberg 2004). In turn, such findings would reinforce the idea that consistent drivers of community structure may persist despite high species turnover. Thus, instead of considering only the difference in species composition among communities, we propose to measure functional -diversity (turnover of biological traits weighted by their abundances) in a highly variable system (estuarine). We specifically investigated whether a ubiquitous functional structure in fish communities may emerge across space and time despite high species turnover.

Recently, Hardy and Senterre (2007) presented a new statistical framework partitioning phylogenetic diversity into α and γ components. Their measures are based on the Rao's quadratic entropy (Rao 1982) and include species relative abundances and phylogenetic distances between species pairs. This framework was partly modified by Villéger and Mouillot (2008) who suggest that the β-component of the quadratic entropy may be used to measure functional turnover among communities, i.e. the functional differentiation among communities, by including species abundances and traits. Functional β-diversity would be low when communities have proportional abundances for similar trait values (whatever species composition) while it would increase when communities tend either to have different trait values or to have different abundances for similar trait values (Villéger and Mouillot 2008). In addition, the amount of functional β-diversity observed in a metacommunity or along a gradient can also be compared to those obtained under a null model to determine whether the functional structure of communities is the result of chance following stochastic processes (neutral theory *sensu* Hubbell 2001) or, at the opposite, is the result of deterministic processes related to the niche theory (e.g. Norberg 2004). Here, we propose to disentangle these two theories of community assembly rules by studying the levels of functional β-diversity among estuarine fish communities (Terminos lagoon, Gulf of Mexico) under highly fluctuating environmental conditions.

Fish communities inhabiting tropical estuaries provide unique opportunities to investigate functional diversity partitioning because (*i*) fish functional traits have already revealed mechanisms underlying community structure (e.g. Mason et al. 2008), (*ii*) tropical communities are generally rich and such species-rich communities are necessary to implement null models of community structure and (*iii*) estuaries have high variability in environmental conditions (mainly salinity) which forces a high species turnover across space and time (e.g. Sosa-Lopez et al. 2007). Moreover, tropical estuarine ecosystems are of primary concern for human population welfare since they provide various services of high value (protein source, regulation of pollution, recreational areas) while human activities severely impact them (Costanza et al. 1997). Moreover, fishes (teleosts and rays) have a large range of morphologies, life-history traits, behaviours, and diets, and are central in controlling fluxes of matter and energy within aquatic systems (Holmlund and Hammer 1999). For instance, a loss of fish diversity may alter nutrient recycling (McIntyre et al. 2007) and may weaken ecosystem resilience (Bellwood et al. 2004).

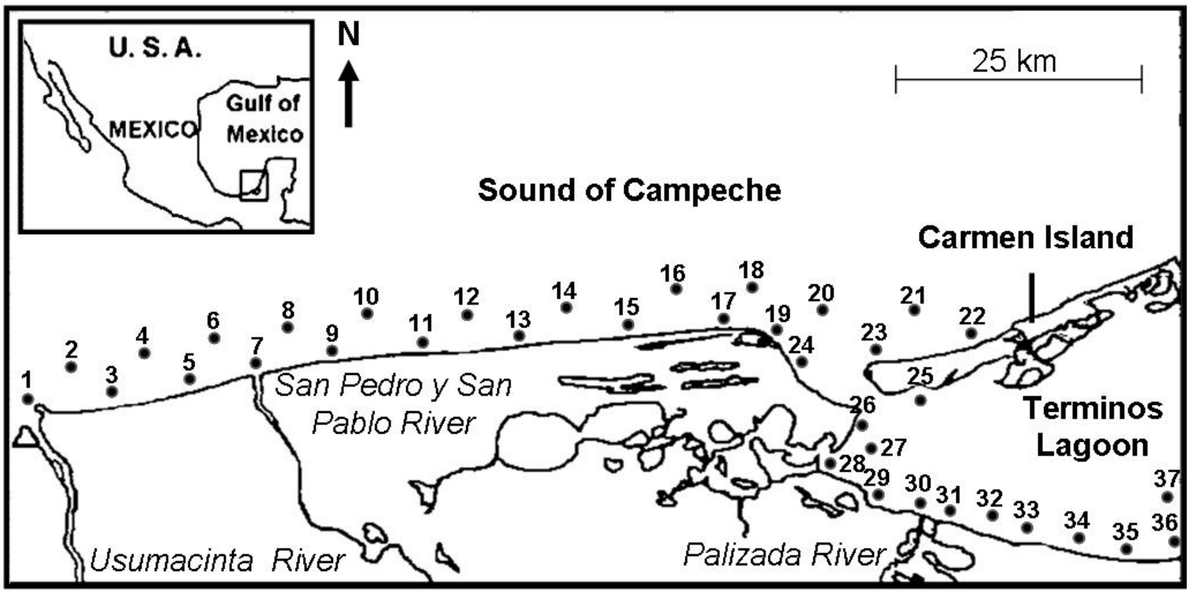
To our knowledge measuring functional β-diversity among communities was never achieved. Towards this objective, we collected a large dataset of estuarine fish communities, we measured a new set of functional traits related to fish diet and fish locomotion, and we proposed a new framework that allows the decomposition of functional diversity into α, γ and β-components including turnover in functional traits and in species abundance compositions. We further tested whether the observed level of functional β-diversity among communities can be expected by chance following random trait assignments, or whether it is due to non random species replacements among communities.

Material and methods

The study system

The study area was located in the south of the Gulf of Mexico along the coast of the Campeche State (Mexico) (Appendix A). We focused on a 150-km long transect (18°37’16N - 92°42’28W to 18°30’20N - 91°28’03W) of 37 stations distributed in the south-western part of the Terminos Lagoon and along the adjacent coast (Villéger et al. 2008). This transect crossed the discharge of three main rivers (the Usumacinta, San Pedro y San Pablo, and Palizada rivers) and the Carmen inlet, i.e. the exit of the Terminos Lagoon flow. Local environmental conditions were highly variable through space and time. For example, salinity ranged from 0 to

42 psu, depth from 0.8 to 12 meters and transparency from 0 to 100% of the water column depth (Villéger et al. 2008).



Appendix A Location of the study area and of the 37 sampled stations.

Sampling protocol

We conducted two sampling campaigns, one from February 2003 to January 2004 and the other from February 2006 to January 2007. No major environmental changes were noticed between these two campaigns which were used as replicates to reinforce the robustness of our findings. Each campaign consisted in a monthly biological survey of the 37 stations (Appendix A) localized using a Global Positioning System with a precision of 75 m. Fish communities were sampled using a shrimp-trawl (length: 5 m, mouth opening diameter: 2.5 m, mesh size: 19 mm) towed 12 minutes at a constant speed of 2.5 knots. The volume sampled was thus of 4,500 m^3. This active sampling method is well adapted to fishes living in this shallow coastal area since they are relatively small (<30cm) and slow swimmers. For each sample, all individuals were identified at the species level and weighed to the nearest decigram.

Ecomorphological traits

For several decades, many studies have focused on the assessment of fish ecological niches through eco-morphological traits (e.g. Gatz 1979; Wainwright et al. 2002; Boyle and Horn 2006). During the 2006-07 sampling campaign, a maximum of 20 individuals by species were randomly selected. On each of these individuals, 17 morphological and 2 anatomical traits were measured (Figure 1). Fish mass was measured using an electronic balance (precision 0.1g). Body width, mouth width and mouth depth were measured using an electronic caliper (precision of 0.1mm). The 14 other morphological traits were measured on digital pictures with a precision of 0.1 mm (camera: Canon Powershot G6, resolution: 7 millions of pixels) thanks to the software ImageJ. The length of the longest gill raker was estimated using a stereomicroscope (precision of 0.1mm). The gut (from the esophagus to the anus) was extracted by dissection, stretched and measured to the nearest millimeter.

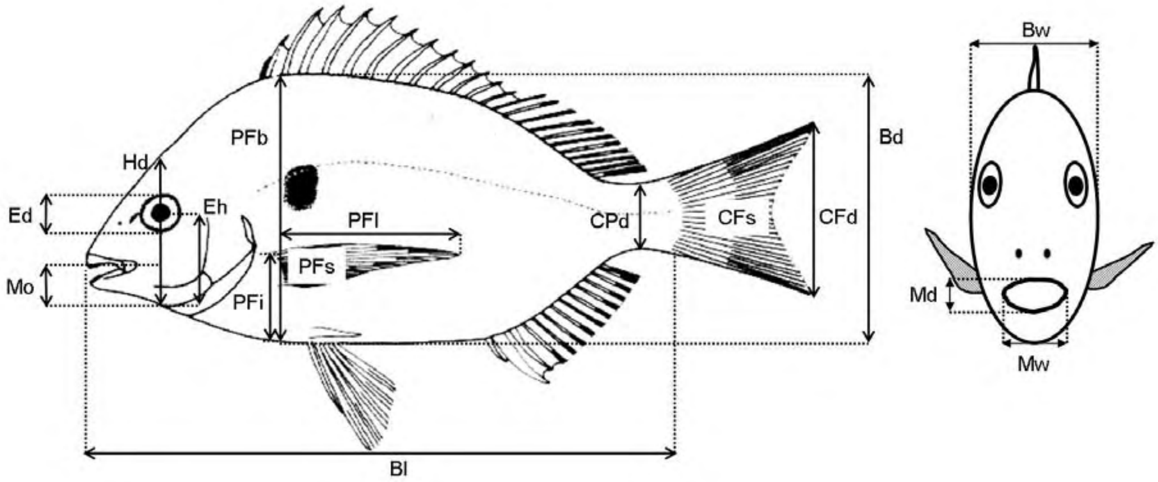


Figure 1. Morphological traits measured on digital pictures (a): *Bl* body standard length, *Bd* body depth, *CPd* caudal peduncle minimal depth, *CFd* caudal fin depth, *CFs* caudal fin surface, *PFi* distance between the insertion of the pectoral fin to the bottom of the body, *PFb* body depth at the level of the pectoral fin insertion, *PFl* pectoral fin length, *PFs* pectoral fin surface, *Hd* head depth along the vertical axis of the eye, *Ed* eye diameter, *Eh* distance between the centre of the eye to the bottom of the head, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis ; and with an electronic caliper (b) : *Bw* body width, *Md* mouth depth, *Mw* mouth width.

For flatfishes, body depth and width, mouth depth, width and position, and eye position were measured relatively to the position of the fish in its environment; in other words, the lateralization was not considered.

After standardization and estimation of ratios, these morpho-anatomical traits yielded 16 functional traits involved with two activities: food acquisition (7 traits) and locomotion (10 traits), the logarithm-transformed body mass being common to the two functions (Table 1). From these 16 traits, three are novel while five were adapted from previously proposed traits. All these traits are measurable at the individual level and, for each function, the set of traits aims to quantify as well as possible the functional niche of species.

Table 1 List of 16 functional traits, abbreviations, formula and relevance for each function of interest. For the two functions, the logarithm of body mass, log (Mass+1), was also considered as a functional trait. Description of morpho-anatomical measures and corresponding codes are presented in figure 1.

	Functional trait	Code	Formula	Function
Food acquisition	Oral gape area	***Osf***	$\frac{Mw \times Md}{Bw \times Bd}$	Relative to maximum prey size or ability to water filtering (adapted from Karpouzi and Stergiou 2003)
	Oral gape shape	***Osh***	$\frac{Md}{Mw}$	Relative to prey shape (Karpouzi and Stergiou 2003)
	Oral gape position	***Ops***	$\frac{Mo}{Hd}$	Relative to position of preys in the water column (adapted from Sibbing and Nagelkerke 2001)
	Gill raker length	***GRlst***	$\frac{GRl}{Hd}$	Relative to filtration capacity or gill protection (adapted from Sibbing and Nagelkerke 2001)
	Gut length	***Glst***	$\frac{Gl}{Bl}$	Relative to digestibility of food (Kramer and Bryant 1995)
	Eye size	***Edst***	$\frac{Ed}{Hd}$	Relative to prey detection (adapted from Boyle and Horn 2006)
Locomotion	Eye position	***Eps***	$\frac{Eh}{Hd}$ *	Relative to position in the water column (Gatz 1979)
	Body transversal shape	***Bsh***	$\frac{Bd}{Bw}$	Relative to position in the water column and hydrodynamism (Sibbing and Nagelkerke 2001)
	Body transversal surface	***Bsf***	$\frac{\ln\left(\left(\frac{\pi}{4} \times Bw \times Bd\right)+1\right)}{\ln(Mass+1)}$	Relative to mass distribution along the body and hydrodynamism
	Pectoral fin position	***PFps***	$\frac{PFi}{PFb}$ o	Relative to maneuverability and position in the water column (Dumay et al. 2004)
	Aspect ratio of the pectoral fin	***PFar***	$\frac{PFl^2}{PFs}$ o	Relative to propulsion and/or maneuverability (adapted from Fulton et al. 2001)
	Caudal peduncle throttling	***CPt***	$\frac{CFd}{CPd}$	Relative to swimming endurance (Webb 1984)
	Aspect ratio of the caudal fin	***CFar***	$\frac{CFd}{CFs}$ #	Relative to endurance, acceleration and/or maneuverability (Webb 1984)
	Fins surface ratio	***Frt***	$\frac{2 \times PFs}{CFs}$ #	Relative to the swimming type (pectoral or caudal fin propulsion)
	Fins surface to body size ratio	***Fsf***	$\frac{(2 \times PFs)+CFs}{\frac{\pi}{4} \times Bw \times Bd}$	Relative to endurance, acceleration and/or maneuverability

* for flatfishes, $Eps = \frac{2 \times Ed}{Hd}$ as the two eyes are on the "top" of the head

^{O} flatfishes were considered without functionally pectoral fins, so *PFps* and *PFar* were fixed to 0

$^{\#}$ for species without caudal fin, *CFar* and *Frt* were fixed to 0

Indeed, food acquisition and locomotion are complex functions that cannot be assessed using few traits only (Dumay et al. 2004; Bellwood et al. 2006; Mason et al. 2007). For example, swimming ability combines several performances such as speed, endurance and maneuverability (Webb 1984) and thus cannot be summarized using one functional trait only (e.g. the swimming factor of Olden et al. (2006)). Moreover, our set of traits is not designed for a restricted taxa, family or morphological type but, instead, aims at being applied to all ray-finned fishes, sharks and rays species, so potentially all fish communities in fresh and marine waters. However, for particular morphologies (species without tail, flatfishes, rays), conventions were used for morphological measures (Figure 1) and functional trait estimations (Table 1).

For each species, the mean trait values were finally computed from individual measures assuming that intraspecific variations were lower than interspecific variations (Dumay et al. 2004). Then, for each trait, mean values were standardized so that the mean was 0 and standard deviation was 1. Functional distances among fish species pairs were estimated using the Euclidean distance on standardized functional trait values. Some fish species were very rare and were not captured in sufficient number during the 2006-07 campaign, preventing a correct estimation of their functional traits. Thus, among the 888 sampling points (2 years x 12 months x 37 stations), only those whose 80% of the biomass was represented by species functionally characterized were kept for analysis. For the samples matching this criterion, the biomass belonging to species not functionally characterized was removed. Consequently, those rare species were not included in our study but their low biomass would marginally influence the estimations of our functional diversity components that are based on abundances.

Partitioning functional diversity into α, β and γ components

We studied functional turnover among fish communities belonging to the same stratum. These strata were defined both through time (between months for a given site) and space (between sites for a given month). Thus, for each of the two periods (2003-2004 and 2006-2007), sampling points were grouped into spatial strata (37 stations for each month) and temporal strata (12 months for each station).

To estimate functional turnover we used the decomposition of the Rao’s quadratic entropy index developed by Villéger and Mouillot (2008). For each of the N sampling points of the stratum, α -diversity based on the Rao's quadratic entropy was computed for the k^{th} sample as:

$$\alpha_k = \sum_{i=1}^{S_k}\sum_{j=1}^{S_k}\delta_{ij}\, p_{ik}\, p_{jk}$$

S_k is the number of species in the sample k. δ_{ij} is the Euclidian distance between species i and j according to their respective standardized trait values for the considered function. The relative abundance p_{ik} was obtained from the biomass b_{ik} of species i for the sample k with $p_{ik} = \frac{b_{ik}}{\sum_{l=1}^{S_k} b_{lk}}$

For each stratum, the mean α-diversity ($\overline{\alpha}$) was calculated by: $\overline{\alpha} = \sum_{k=1}^{N} f_{.k}\alpha_k$

where N is the number of samples in the stratum, α_k is the α-diversity of sample k and $f_{.k}$ is the relative abundance of sample k in the stratum, $f_{.k} = \frac{b_k}{\sum_{k=1}^{N} b_k}$ where b_k is the total biomass in sample k: $b_k = \sum_{i=1}^{S_k} b_{ik}$

The γ -diversity was: $\gamma = \sum_{i=1}^{S}\sum_{j=1}^{S}\delta_{ij}\, p_{i.}\, p_{j.}$, where S is the number of species contained in the entire stratum while $p_{i.}$ is the relative abundance of species i in the stratum, $p_{i.} = \sum_{k=1}^{N} f_{.k}\, p_{ik}$

Following the additive partition of diversity $\gamma = \beta + \overline{\alpha}$ proposed by Ricotta (2005) and detailed in Villéger and Mouillot (2008), β-diversity was deduced from γ and $\overline{\alpha}$ for each stratum by:

$$\beta = \gamma - \overline{\alpha} = \sum_{i=1}^{S}\sum_{j=1}^{S}\delta_{ij}\, p_i.p_{j.} - \sum_{k=1}^{N} f_{.k}\alpha_k$$

This value was then standardized by γ (Hardy and Senterre 2007) to be constrained between 0 and 1: $\beta* = \frac{\beta}{\gamma}$. Villéger and Mouillot (2008) demonstrated that $\beta*$ tends to zero when close trait values have the same relative abundances in all the communities, i.e. when all the communities share a common functional structure. At the opposite $\beta*$ increases when the communities do not share the same traits and/or do not have the same abundance distribution among the traits.

In parallel to the estimation of functional β-diversity we estimated, for each stratum (year x variable x station or month), the turnover in species composition (β^*_{sp}) which is computed as (Lande 1996):

$$\beta^*_{sp} = 1 - \frac{\sum_{k=1}^{N} R_k}{N \times R_{stratum}}$$

where $R_{stratum}$ and R_k are respectively the species richness in the whole stratum and in sample k. Thus when the N samples have no species in common, $R_{stratum}$ is equal to the sum of R_k and consequently β^*_{sp} tends to 1. At the opposite, if all the samples share the same species, $R_{stratum}$ is equal to R_k and β^*_{sp} is 0.

Testing assembly rules

There is a limited ecological meaning to interpret β index values *per se*. Instead, one needs to assess whether the measured values of β are significantly different from those expected under suitable null hypotheses. Here, we aimed to test whether spatial and temporal functional turnovers observed among fish communities were due to random associations between functional identities and abundances. To address this issue, we designed an appropriate null model following Stubbs and Wilson (2004). For each sample of the studied stratum, observed abundances were assigned to species at random without replacement. This procedure actually randomizes the distribution of abundances among functional identities which basically assigns the functional distances between species pairs at random without replacement. Additionally, we controlled a posteriori the randomization procedure so that species richness of each stratum remains the same as the observed one. In other words, random assignments which lead to the loss of species from the species pool were not allowed. Therefore, using this procedure we maintained observed community structures (same richness, same abundance distribution between species in each sample and same abundance distribution between samples). We also avoided any bias related to spatial and temporal autocorrelation (Stubbs and Wilson 2004). Moreover, there is no reason to expect that the presence of dominant-ubiquitous species artificially decreased functional β-diversity since the level of taxonomic β-diversity among communities (β^*_{sp}) was not modified by the null model.

Then, for each stratum, 999 randomizations were carried out and then observed functional β-diversity values β^*_{obs} were compared to the distribution of the functional β-diversity values obtained under the null hypothesis (β^*_{H0}). Finally, the proportion of $\beta^*_{H_0}$ lower (or higher) than β^*_{obs} provides the p-value which is the type I error (probability of rejecting the null hypothesis whereas it is true (Manly 1998)). Thus, considering a two-sided test with a global risk of 5%, a *p*-value lower than 2.5% indicated a functional β-diversity lower than expected whereas a *p*-value higher than 97.5% indicated a functional β-diversity higher than expected.

The Index of Variance (IV) of Zobel et al. (1993) was used to compare β^*_{obs} with the mean $\beta^*_{H_0}$ expected under the null model ($\overline{\beta^*_{H_0}}$): $IV = 2 \times \left(\frac{\beta^*_{obs}}{\beta^*_{obs} + \overline{\beta^*_{H_0}}} \right) - 1$. IV provides a standardized index for expressing the ratio between observed and expected values of a statistic. It ranges between -1 and 1. A negative value indicates that the observed value is less than the expected value, whereas a positive one indicates that the observed value is greater than the expected value.

According to the standardized trait values, 20 functional groups were clustered for the two functions of interest. For each function, the dominance of the groups was explored in terms of abundance and occurrence both at sample and stratum scales. To visualize the functional structure of fish communities, we carried out a Principal Component Analysis (PCA) on the species X traits matrix for each function of interest. Indices computing and statistical analysis were carried out using R statistical software (R Development Core Team 2008).

Results

Data collected

A total of 46,012 and 25,639 individuals were respectively caught in 2003-2004 and 2006-2007 for respective weights of 557 and 398 kg. Species richness was 87 for both periods while total species richness was of 105 species. The 19 eco-morphological measures were estimated on 1021 individuals belonging to 70 species. Among these 70 species, the 15 functional traits were estimated on 20 individuals for 40 species and on more than 10 individuals for 50 species.

Finally, 113 samples out of the initial 888 samples were excluded because for 62 samples the net was empty, for 36 there was just one species and for 15 the biomass of species functionally characterized was less than 80%.

Taxonomic vs. functional turnover

Species β-diversity (β^*_{sp}) was globally high (Table 2), ranging in the 98 strata (2 years x (12 months+ 37 sites)) between 0.669 and 0.887. Conversely, functional β-diversity (β^*_Q) was globally low (Table 2), ranging for the 98 strata and for the two functions between 0.063 and 0.617.

Comparisons between observed and simulated values of β-diversity thanks to the index of variance (IV) show that IV values for functional β-diversity (β^*_Q) were mainly negative (Figure 2) with a mean of -0.169 ±0.167 (only 23 IV values were positive out of 196). Moreover, these low functional β-diversity values were significantly lower than expected under the null model ($p<0.025$) in 58% of the strata (Table 2) while functional β-diversity values were never significantly higher than predicted by chance. Taken together, these results demonstrate that, through space and time, functional turnover among fish communities was generally low while taxonomic turnover was high.

Table 2. Summary (mean ± standard deviation) of observed *β*-diversity values for each function, variable and index. β^*_{Sp} is the taxonomic *β*-diversity computed on species composition with the Lande's index. β^*_{Q} is the *β*-diversity computed with the quadratic entropy on biomasses. β^*_{Qwc} is the *β*-diversity computed with the quadratic entropy on biomasses but without considering species belonging to the two core functional groups. The three last columns present the comparisons between observed *β*-diversity values (β^*_{obs}) and *β*-diversity expected under the null model ($\beta^*_{H_0}$**),** expressed as the percentage over all the studied strata. The test is two-sided with a global level of significance of 0.05.

Function	Strata	Index	*β*-diversity	Significantly lower (%)	No significantly different (%)	Significantly higher (%)
Food acquisition	spatial	β^*_{Sp}	0.827 ±0.021			
		β^*_{Q}	0.33 ±0.061	83.33	16.67	0.00
		β^*_{Qwc}	0.427 ±0.075	4.17	87.50	8.33
	temporal	β^*_{Sp}	0.715 ±0.037			
		β^*_{Q}	0.232 ±0.094	60.81	39.19	0.00
		β^*_{Qwc}	0.345 ±0.107	31.08	67.57	1.35
Locomotion	spatial	β^*_{Sp}	0.827 ±0.021			
		β^*_{Q}	0.335 ±0.07	66.67	33.33	0.00
		β^*_{Qwc}	0.448 ±0.103	16.67	79.17	4.16
	temporal	β^*_{Sp}	0.715 ±0.037			
		β^*_{Q}	0.24 ±0.096	44.59	55.41	0.00
		β^*_{Qwc}	0.377 ±0.121	22.97	77.03	0.00

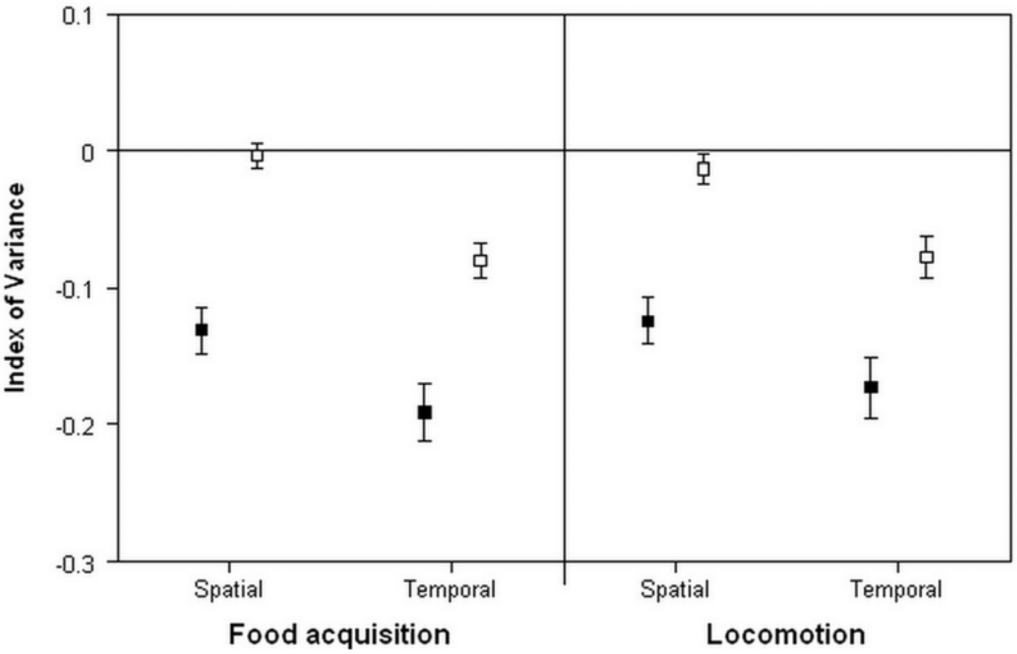


Figure 2. Index of variance (IV) between observed and simulated (under the null model) β-diversity values with IV being bounded between -1 and 1. A negative IV value indicates that the observed β-diversity is lower than expected at random.
For the two functions and the two variables studied, IV mean values and standard errors over all the strata are plotted for the two indices: IV for functional β-diversity (βQ) are black squares whereas IV for functional β-diversity without considering biomasses of species belonging to the two core functional groups (βQwc) are white squares.

Core vs. satellite functional groups

Fish biomass was unevenly distributed among species and among functional groups revealing the presence of some core functional groups, which consistently dominated fish communities across space and time, while many satellite functional groups shared a low proportion of total biomass. Indeed we divided the 70 species into 20 groups and we plotted a rank frequency diagram showing the decreasing biomass along ranked functional groups (Figure 3).

This graph reveals similar patterns for the two functions considered (food acquisition and locomotion): a strong dominance of few groups which were frequent and abundant and a right-skewed tail containing many rare groups. Among the 20 groups clustered for each function, the two most abundant groups represented respectively 57 and 65% of the total biomass while they only contained 10 and 16 species (out of 70), respectively. These groups also occurred very frequently (present in more than 75% of the 775 samples).

More generally, for the two functions, we found only five groups with a relative abundance higher than 5%. Interestingly, these groups also occurred in more than one fourth of the samples. For the two functions, the most abundant group pooled the three sea catfishes (Ariidae species *Cathorops melanopus*, *Ariopsis felis* and *Bagre marinus*) which accounted, on average, for 35% of the total biomass. The second group was mainly composed of Sciaenidae species (in particular *Stellifer lanceolatus*, *Bairdiella chrysoura* and *Cynoscion arenarius and C. nothus*).

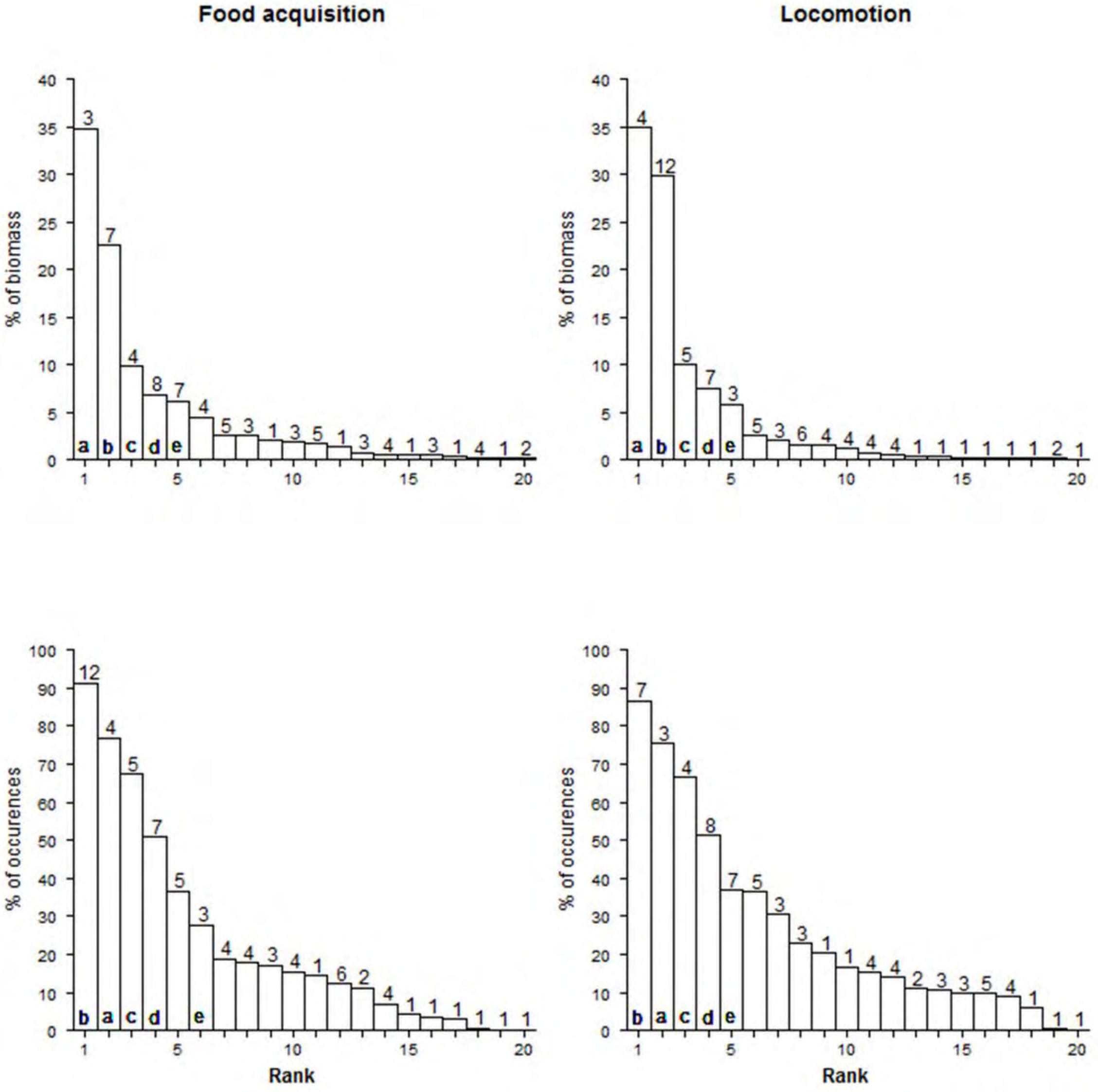


Figure 3. Rank-frequency diagrams representing relative abundances (top) and occurrences (bottom) of the 20 functional groups obtained for each of the two functions: food acquisition (left) and locomotion (right). The relative abundance is the mean relative biomass of the group. The relative occurrence is computed over the 775 stations studied for each functional group. The five most abundant groups for each function are named with letters (a-e) in the two plots. Species richness by functional group is reported above the bars.

Figure 4 represents the distribution of the 15 most abundant species (in term of mean relative abundance per sample) in the functional space for each function (summarized by the first plan of the Principal Component Analysis). These species contributed to 81% of the total biomass and one of them was the most abundant in 687 out of the 775 samples, and in all spatial and temporal strata. The PCA clearly highlights the presence of core functional groups. First, some parts of the functional space are empty and some others are marginally occupied by rare species (symbolized by black crosses). Secondly, some parts of the functional space contain several abundant and frequent species functionally close such as the three species of sea catfishes and the sciaenids (the two weakers *Cynoscion arenarius* and *C. nothus* and the American Stardrum *Stellifer lanceolatus*). The three sea catfishes occupied the first, fourth and fifth rank in terms of mean relative biomass. The most abundant of these species, the Dark Sea Catfish *Cathorops melanopus* was present in only 420 of the 775 samples whereas the “sea catfish” group is present in 585 samples. This species has the highest biomass in 214 samples whereas the “sea catfish” group was the most abundant in 344 (food acquisition) and 323 (locomotion) samples. It indicates that there was a replacement of these species across space and time which allowed the dominance of that group whatever the species composition. The same pattern was true for the “sciaenid” group which contains many species. The American Stardrum *Stellifer lanceolatus* was the most widespread species (525 occurrences) but was not often the most abundant (91 samples). However the “sciaenid” group was the dominant group in 185 and 244 samples for food acquisition and locomotion.

To assess the composition turnover intra core functional groups we estimated the Bray-Curtis dissimilarity index between sample pairs in each stratum. The Bray-Curtis dissimilarity index was consistent across strata, for the two functions and for the two core functional groups with a mean of 0.720 ±0.115 for food acquisition and of 0.749 ±0.103 for locomotion. This clearly demonstrates that the dominance of the core functional groups was not only determined by one ultra dominant species but, instead, by a set of species which alternatively dominate inside each group across space and time.

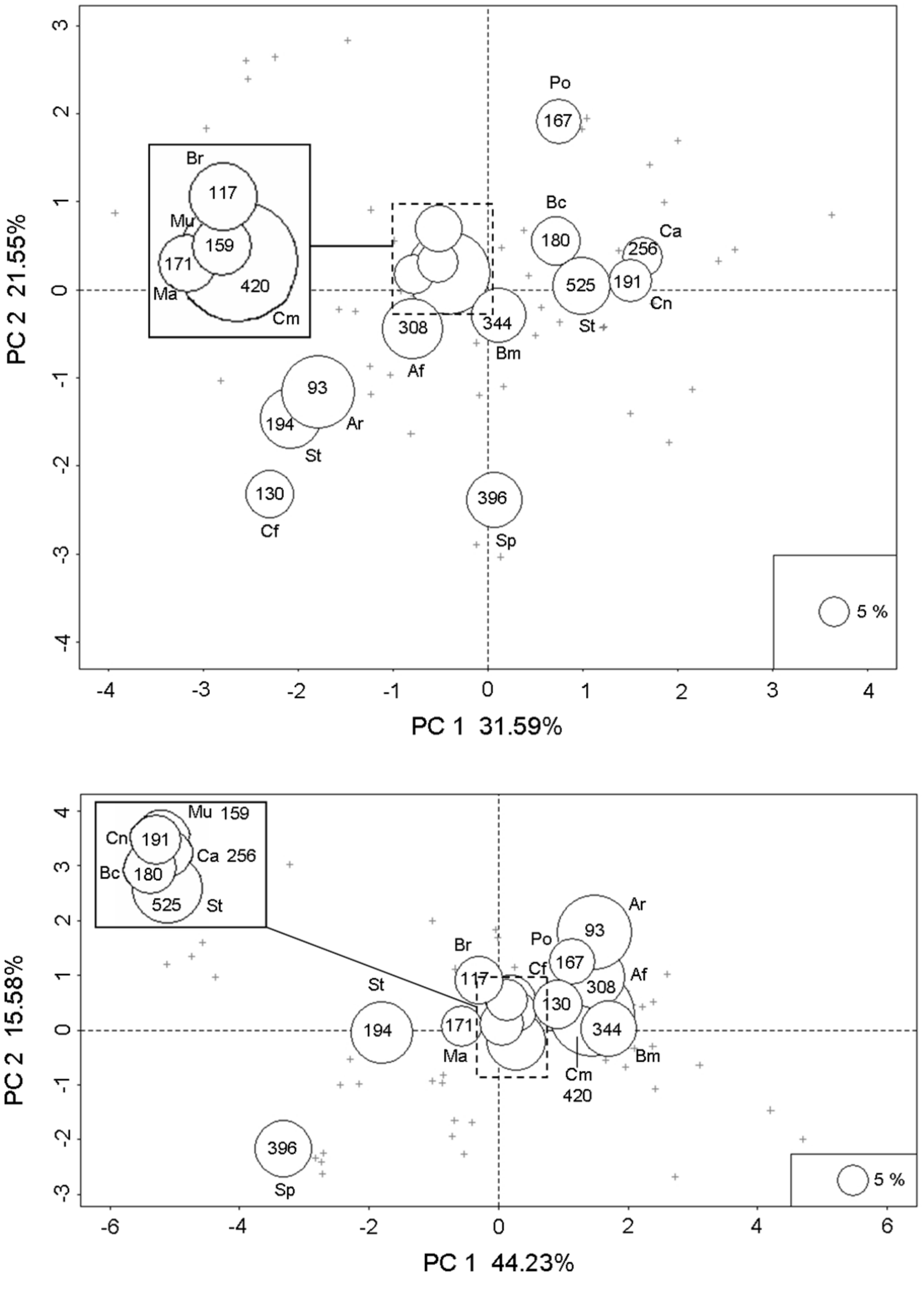


Figure 4. Biplot of the Principal Component Analysis (PCA) carried out using the functional traits of 70 species for each function of interest. The 15 dominant species are represented by circles. Their mean relative biomass when they occur is proportional to the surface inside the white circles. Their occurrences over the 775 samples are given in the center. The other 65 species are plotted with black cross.

Codes for species are: Af=*Ariopsis felis*, Ar=*Archosargus rhomboidalis*, Bc=*Bairdiella chrysoura*, Bm=*Bagre marinus*, Br=*Bairdiella ronchus*, Ca=*Cynoscion arenarius*, Cf=*Chaetodipteurs faber*, Cm=*Cathorops melanopus*, Cn=*Cynoscion nothus*, Ma=*Menticirrhus americanus*, Mu=*Micropogonias undulatus*, Po=*Polydactylus octonemus*, Sl=*Stellifer lanceolatus*, Sp=*Symphurus plagiusa*, St=*Sphoeroides testudineus*,

Functional turnover without core groups

To test whether low functional turnover (β_Q^*) among fish communities was due to the presence of these core functional groups we ran the same randomization procedure excluding species belonging to the two most abundant groups in term of biomass (respectively 10 and 16 species for the two functions). The samples with less than two species after the removing procedure were not included (respectively 93 and 143 for the two periods). The results are provided in Table 2 and Figure 2. The IV index values were very close to zero with a mean of -0.061 ±0.111 and more than 134 IV index values (out of 196) had a value between -0.1 and 0.1. Moreover, for 76% of the 196 strata, functional β-diversity without core functional group (β_{Qwc}^*) was not significantly different from the values expected by chance.

The percentage of strata where β-diversity was lower than expected by chance dropped from 58% (previous analysis including core groups) to 23%. These results show that the pattern of low functional β-diversity observed at the community scale was not reproducible at the scale of satellite functional groups assuming that only core functional groups maintain a low functional turnover among fish communities.

Discussion

Diversity partitioning among scales has been investigated for more than 40 years based on the taxonomic composition of communities (e.g. Legendre et al. 2005), but there are still few studies that explicitly consider biological distances between species. Here, using a new procedure to decompose γ-functional diversity into α and β-components, we demonstrate that a low functional turnover occurs in estuarine fish communities (temporally and spatially) despite high environmental and taxonomic turnover (Table 2). Hence, β-diversity, based on the quadratic entropy, quantifies a new facet of community similarity that deserves to be estimated in many systems to test whether taxonomically dissimilar communities share much more biological similarity than expected before.

Our study suggests that using estuarine fish communities is relevant for assessing functional diversity partitioning across scales. Indeed, like most of estuarine ecosystems

(Blaber 2002), the Terminos Lagoon area is marked by a high environmental variability in terms of water salinity, depth, sediment or organic matter inputs (Villéger et al. 2008). We also found high species richness (more than one hundred species of fish) coupled with a high species turnover both on temporal and spatial scales (around 0.8). The functional approach of the diversity partitioning differs from the taxonomic one by considering functional distances between species pairs. However, as the functional traits are estimated using morpho-anatomical traits, inter-species distances are likely to follow taxonomy. The correlation between taxonomic closeness and functional similarity is especially true between orders. It is obvious for example that Pleuronectiforms are morphologically and thus functionally very different from Perciforms or Siluriforms. On the contrary, when considering the intra-order differences, the relation becomes weaker. For example, for Perciforms, families can be functionally very dissimilar such as Gerreidae (mojarra) and Triglidae (searobin). Furthermore, among Sciaenidae (the richest family in the region), strong functional differences exist between weakers (gen. *Cynoscion*) and kingcroaker (gen. *Menticirrhus*). On the other hand, it is possible to observe functional convergence between two species belonging to two different families: the American Stardrum (*Stellifer lanceolatus*, Sciaenidae) is very similar to the Barred Grunt (*Conodon nobilis*, Haemulidae). Thus, since functional characterization of fish communities does not match perfectly to their taxonomic structure their study deserves attention.

The functional β-diversity values obtained with the Rao's quadratic entropy index clearly indicate an overall low turnover in the functional structure of communities (Table 2). Moreover, these values of β-diversity were globally lower than those expected under the null model (Figure 2).The null hypothesis posits that traits in each community are randomly attributed to species (and their abundances). Therefore, these results together suggest that some sets of trait values are more likely to be associated with the highest abundances, whatever the environmental conditions, the station and the season. Since we kept the observed metacommunity structure (occurrence and abundance of species in each community) within the randomized metacommunities while functional traits were assigned to species at random there is no reason to expect that species with similar sets of traits (functionally related) have the highest abundances in all communities. Indeed, we found for the two functions a strong dominance of two core functional groups. Thus, as the Rao's quadratic entropy index depends mainly on the functional dissimilarities of the most abundant species, the functional β-diversity is maintained at a low level by these species. In addition, we show that, when we remove these two groups from fish communities, functional *β*-diversity values are not different from the null hypothesis in 76% of the cases (Table 2). Hence, these core functional groups, which are dominant in almost all the samples, maintain a ubiquitous functional structure through space and time whatever environmental conditions. Furthermore, these core functional groups are not determined by an ultra-dominant species On the contrary they are structured by several dominant species which replace each others through space and time (Figure 4).

Since ecosystem processes depend on the presence and abundance of organisms with particular functional traits (Ellison et al. 2005; Diaz et al. 2007), there is an urgent need to quantify whether the functional composition of communities varies across space and time. More generally, the finding of repeatable functional structures among communities (low functional *β*-diversity) would suggest that apparently diverse and idiosyncratic assemblages may be ruled by similar ecological mechanisms. On the contrary a high functional *β*-diversity among communities would suggest the predominance of environmentally driven functional structures. Finally the finding of a functional *β*-diversity level similar to those expected by chance would suggest the predominance of stochastic processes (dispersion, neutrality) underlying the functional structure of communities. Overall, our results suggest that communities are not randomly assembled with a predominance of niche-related processes influencing species turnover among communities to keep rather similar functional structures. In turn, this common functional structure may stabilize ecosystem functioning spatially and temporally. Beyond the term core functional groups, we may define these groups as ‘foundation’ functional groups by analogy to the concept of foundation species coined by Dayton (1972) as species which define much of the structure of a community and which modulate and stabilize fundamental ecosystem processes (see also Ellison et al. (2005) for a review). We suggest that, at least in coastal fish communities, these foundation groups consistently shape the world since they form much of its structure and control ecosystem dynamics through their group-specific traits. Hence, measures of functional *β*-diversity provide indications on the processes that structure communities over spatial and temporal scales but, more importantly, it links metacommunity dynamics to fundamental properties such as ecosystem functioning.

More generally, the decomposition of the quadratic entropy into its *α*- *β*- and *γ*-components, using biological distances between species pairs, has the potential to shed light on many macroecological patterns and may contribute to disentangle the effects of dispersal, niche filtering and competitive interactions in metacommunities. Indeed, this decomposition is very complementary to the partitioning of species traits proposed by Ackerly and Cornwell (2007) which quantifies the α (within-community) and β (between-community) components of trait values along environmental gradients. Instead of a trait-by-trait approach we propose a decomposition of functional diversity based on multidimensional functional distances between species pairs. In addition, this decomposition can be used with functional or phylogenetic differences among species (Ricotta 2005; Hardy and Senterre 2007). Future research would gain to combine analyses of β-diversity using variations in species composition, variations in functional structure and variations in phylogenetic structure and to regress each of these biological distances between communities against geographic and environmental distances. More precisely, for analyzing metacommunity structures or biogeographic gradients, the functional and phylogenetic β diversities between communities can be used as a biotic distances and then regressed on environmental or spatial distances using, for instance, generalized dissimilarity models (Ferrier et al. 2007).

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Stable trophic structure across coastal nekton assemblages despite high species turnover

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ABSTRACT: The finding of invariant structures in species assemblages is of primary importance for ecology because it would suggest that, despite species turnover and environmental gradients, some self-organizing principles may shape these assemblages. Tropical estuarine and coastal ecosystems are ideal for investigating patterns in trophic structures because they contain many species and are characterized by a high variability for both biotic and abiotic variables. We used the data from a 150 km long transect in the Terminos Lagoon region (Campeche State, Mexico) where 37 stations were sampled monthly during 1 yr for both abiotic parameters and nektonic assemblages. We then quantified 3 complementary components of trophic diversity (trophic richness, trophic evenness and trophic divergence) and then challenged the idea that some stable structures may emerge. We found that abiotic parameters, space and time have weak explanatory power on trophic diversity indices. We also observed a high species turnover both at local and regional scales, but it was unrelated to the small variations of trophic diversity indices. This stability of trophic structure is partly due to the predominance of the trophic class 3.25 to 3.5, which accounted invariably for between 50 and 60% of the total nekton biomass across space and time. These findings suggest that the species turnover observed in our system is not random but, rather, allows maintenance of the same abundance distribution along the trophic axis. The mechanisms underlying these emergent properties of trophic structures deserve to be investigated through the use of trophodynamic models.

KEY WORDS: Trophic diversity · Trophic level · Environmental gradients · Terminos Lagoon · Gulf of Mexico

INTRODUCTION

Despite the extraordinary complexity of natural systems, some ecologists expect that a few relatively simple laws may govern patterns such as the structure of species assemblages (Hubbell 2001). Uncovering general and repeatable patterns in species assemblages over space and time has been a major focus of research in ecology because identification of such patterns would suggest that apparently diverse and idiosyncratic assemblages may have common principles. Ultimately, the goal of such a comparative approach should be to identify the processes underpinning any observed universal pattern, which in turn would provide crucial knowledge allowing advances in conservation and environmental management (Mouillot 2007).

Trophic ecology has become a fertile area for discussion of intriguing regularities in assemblages of interacting species feeding on each other. After many contradictory investigations about the scale-invariance of trophic chain length, predator/prey ratio and connectance (relative density of links) in food webs (Briand & Cohen 1984, Sugihara et al. 1989, Havens

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1992, Martinez 1992), there has been an emerging consensus about the scale dependence of these trophic structures (Martinez 1994, Deb 1995, Bersier & Sugihara 1997, Bersier et al. 1999). However, the repeatability or the stability of trophic structures over space and time at the same scale of observation is still questionable. Moreover, the trophic structure of an assemblage cannot be fully captured by a single number (such as the connectance or the trophic chain length), and many facets of this structure, including species abundances and the distribution of biomass along trophic levels, have been overlooked due to a lack of adequate descriptors. Thus, the knowledge of the trophic structure of ecological assemblages is still incomplete, and the spatiotemporal stability in these structures remains unexplored. In the present study, using complementary trophic diversity indices, we sought ubiquity in the trophic structure of nekton assemblages in the Terminos Lagoon region (southern Gulf of Mexico) despite high environmental and species turnover.

Coastal lagoon ecosystems are of primary concern for human population welfare because they provide various services of high value (protein source, regulation of pollution and recreational areas), while anthropogenic activities severely impact them (Costanza et al. 1997). Fluctuating environmental conditions on short spatial and temporal scales also mark these ecosystems. This fluctuation is the consequence of low inertia to external events due to shallowness of water masses coupled with an interface position between marine and freshwater bodies (Basset et al. 2006). These ecological systems provide unique opportunities to investigate invariant patterns in the structure of assemblages because the high variability in environmental conditions generates a high species turnover across space and time (e.g. Wagner 1999). In these coastal systems, the nekton, including shrimps, fish, crabs and squids, is a major biological component. These macroorganisms have a large range of life-history traits, migratory behaviors and diets, thus occupying a key position in the flux of matter through space and time (e.g. Holmlund & Hammer 1999). Identifying regularities in the structure of nekton assemblages in such ecosystems could be challenging because it would suggest the predominance of trophic-based processes despite high turnover in species identity and environmental conditions.

The vertical diversity of the food web is a component of biodiversity and plays a role in the productivity and stability of ecosystems (Diaz et al. 2006, Duffy et al. 2007). However, no consensus has emerged about correct estimations of an assemblage's vertical food web diversity, which we designate as 'trophic diversity.' Similarly to functional diversity, trophic diversity cannot be summarized using a single number. Therefore, we chose to estimate various facets of nekton assemblage trophic diversity using the framework of Mason et al. (2005), who defined 3 primary components of diversity (richness, evenness and divergence) with corresponding indices. These indices were based on the trophic level index which is an integrative parameter based on food items and diet composition and thus characterizes the position of species along the trophic chain. Trophic level is available for a great number of nektonic species across taxa, allowing inclusion of all species in studies of taxonomically and functionally heterogeneous assemblages. In addition, trophic level is a key parameter for modeling marine ecosystem functioning (Pauly et al. 2000, Gascuel 2005) or for studying fishery dynamics (Pauly et al. 1998, Pauly & Watson 2005). For instance, the mean trophic level of fishery landings (MTI, Marine Trophic Index) was a relevant indicator demonstrating that we have been 'fishing down marine food webs' (Pauly et al. 1998). However, the mean trophic level refers only to the central position in the distribution of biomass along the trophic chain; in the study of Pauly et al. (1998), the variability of the biomass distribution along this trophic chain was not included. Therefore, the purpose of the present study is to quantify biomass distribution along the trophic axis by introducing a new set of trophic diversity indices: trophic richness, trophic evenness and trophic divergence.

As an application, we estimated these indices for the nekton assemblages of the Terminos Lagoon region and investigated their variations. In particular, we analyzed how trophic diversity varies with environmental conditions and through space and time. Then we tested the ubiquity of the trophic structure in relation to species turnover and at 2 scales of observation (local to regional).

MATERIALS AND METHODS

Study area. The study area is located along the southern coast of the Campeche State (Mexico) (Fig. 1). The Terminos Lagoon, which is 70 km long and 30 km wide, highly influences this part of the Gulf of Mexico. This wetland ecosystem is of ecological interest for flora and fauna and for terrestrial and aquatic biota. Several anthropogenic factors have affected it in past decades, including the development of intensive farming with concurrent deforestation of mangroves, intensive shrimp fishing, offshore oil extraction and the urbanization of Carmen Island (Ramos Miranda et al. 2005a). Moreover, previous studies have identified a shift from hypohaline to euhaline/hyperhaline conditions in the lagoon (salinity has been

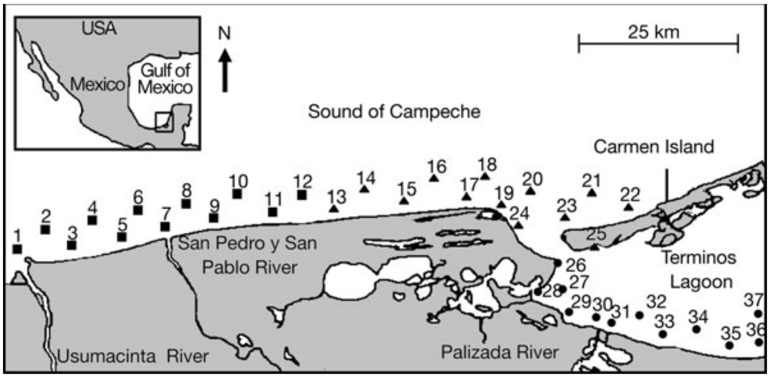

Fig. 1. Study area and 37 sampled stations. Symbols indicating each station depend on the spatial group to which the station belongs (see Fig. 3): (J) Coast 1, (M) Coast 2 and (d) Lagoon

increasing from 24.67 PSU in the 1980s to 26.8 PSU at the end of the 1990s) combined with a decreasing water depth (Ramos-Miranda et al. 2005b, Sosa-López et al. 2005).

The present study focuses on a 150 km long transect (18° 37’ 16” N, 92° 42’ 28” W to 18° 30’ 20” N, 91°28’03” W) including 37 stations distributed in the southwestern part of the Terminos Lagoon and along the adjacent coast (Fig. 1). This transect crosses the discharge of 3 main rivers (the Usumacinta, San Pedro y San Pablo and Palizada rivers) and the Carmen inlet, the exit of the Terminos Lagoon flow (David & Kjerfve 1998).

Sampling protocol. We conducted a monthly biological survey of the 37 stations from February 2003 to January 2004 (Fig. 1), locating sampling points using a Global Positioning System with a precision of 75 m. The survey included both abiotic and biotic parameters. We recorded environmental variables such as water temperature, salinity, pH and dissolved oxygen for the top and bottom of the water column using Hydrolab HL 2011 equipment. Additionally, we measured depth and water transparency using a Secchi disk.

Nektonic assemblages were sampled using a shrimp trawl (length: 5 m, mouth opening diameter: 2.5 m, mesh size: 19 mm) towed 12 min at a constant speed of 2.5 knots. The volume sampled was thus 4500 m^3. Individual organisms were kept in ice on the boat before being frozen. For each sample, all individuals were identified to the species level using the keys of Fischer (1978), Castro-Aguirre (1978) and Resendez Medina (1981a,b), and weighed to the nearest dg.

For each fish species, the trophic level index value (TL) was recorded according to FishBase (Froese & Pauly 2006). For invertebrates (shrimps, crabs, mantis shrimp and squids), we used the trophic level recorded in FishBase (Froese & Pauly 2000) at the best taxonomic level available.

Trophic diversity indices. Functional diversity could be seen as the distribution of functional trait values and of abundance among entities in a given space, entities being either species at the community level or individuals at the population level. In the present study, we focused on the nekton trophic diversity by considering the trophic level as a functional trait. Following Grime (1998), who proposed the biomass ratio effect, we chose biomass as the most relevant measure for abundance; therefore, trophic diversity could be seen as the distribution of biomass along the trophic level axis (Fig. 2). As with species biodiversity, which can be split into different facets (e.g. species richness and evenness, Purvis & Hector 2000), functional diversity was split into 3 complementary components (Mason et al. 2005): richness, evenness and divergence. We applied these 3 components to the distribution of abundance along a trophic axis to obtain a measure of trophic richness, trophic evenness and trophic divergence.

Trophic richness represents the proportion of the trophic chain an assemblage fills. It could be estimated by either the number of trophic levels (trophic richness sensu stricto) or the maximum range of trophic levels (length of the trophic chain) present in a nekton assemblage (Fig. 2). These 2 indices are complementary and potentially unrelated. For instance, the range can be high with the presence of only 2 extreme trophic levels (1 at each side of the trophic chain), whereas an assemblage with many species having close trophic levels will show a relatively small range.

Trophic evenness describes how equitably distributed the biomass is along the trophic axis. It includes both the regularity of the distribution of values along the trophic axis and the evenness of the abundance among these trophic levels. The functional regularity index (FRO) proposed by Mouillot et al. (2005) includes these 2 aspects. In the present study, we used a standardized version of the proposed index: for an assemblage of S species, TL and corresponding biomass (w) were ranked increasingly to compute S–1 weighted evenness differences (EW) for species i and j using:

$$EW_l = \frac{TL_i - TL_j}{w_i + w_j} \qquad (1)$$

where l represents the S–1 pairs of species. These values were then standardized to a percentage weighted evenness:

$$PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l} \qquad (2)$$

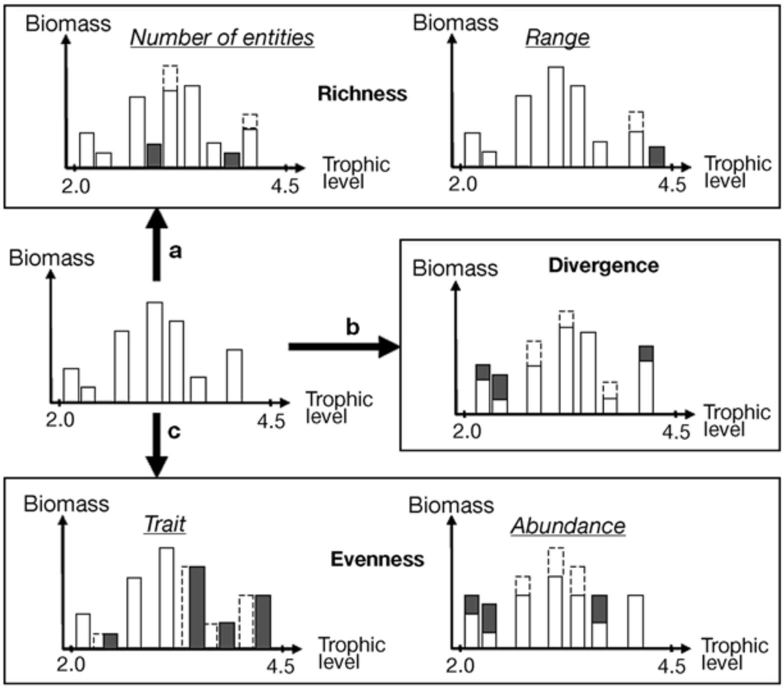

Fig. 2. Theoretical presentation of trophic diversity components. From a hypothetical assemblage, an increase of each trophic diversity component is illustrated in 3 directions: (a) increase in trophic richness with either an increase in the number of entities (left) or an increase in the range of trophic level values (right); (b) increase in trophic divergence due to a shift of biomass from the middle of the trophic axis to extremities; or (c) an increase in trophic evenness with either an increase in the regularity of the distribution of the trophic level values along the axis (left) or an increase in the regularity of biomass among these trophic level values (right)

In the case of perfect regularity of abundance distribution along the trophic axis, all EW_l would be equal and all PEW_l values would be $(S–1)^{-1}$. Conversely, when PEW_l values differ, trophic evenness must decrease. To this aim we compared PEW_l values to $(S–1)^{-1}$ to obtain the FRO index:

$$FRO = \frac{\sum_{l=1}^{S-1} \min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}} \qquad (3)$$

This index is designed to be independent of the trophic richness and is constrained between 0 and 1. The value 1 is obtained when all PEW_l are equal to $(S–1)^{-1}$. Trophic evenness of a community would be high if coexisting species have regularly spaced trophic levels with similar biomass (Fig. 2).

Trophic divergence quantifies the divergence of the nekton biomass distribution from the mean trophic level of the assemblage (Fig. 2). It is therefore correlated with niche differentiation and may indicate the potential resource use spectrum and intensity of competition. For example, with a maximum biomass near the mean trophic level value, trophic divergence would be low. Conversely, trophic divergence would be high if biomass density peaks at the extremities of the trophic axis. We estimated trophic divergence with the FD_{var} index of Mason et al. (2003). FD_{var} is based on an abundance-weighted sum of squares analogous to a log-transformed variance:

$$FD_{var} = \frac{2}{\Pi}\arctan(5V),$$

$$\text{with} \quad V = \sum_{i=1}^{S} w_i \times (\ln TL_i - \overline{\ln TL}) \qquad (4)$$

$$\text{where} \quad \overline{\ln TL} = \sum_{i=1}^{S} w_i \times \ln TL_i$$

By design, FD_{var} is independent of species richness and constrained to the 0 to 1 range.

Statistical properties of the indices were already investigated in previous papers (Mason et al. 2003, Mouillot et al. 2005). These 4 trophic diversity indices were computed using R software (R Development Core Team 2007).

Statistical analysis. Sampling points with fewer than 3 trophic levels in the assemblage were removed from statistical analysis. Indeed, with only 1 trophic level, trophic range, trophic evenness and trophic divergence do not make sense. For samples with only 2 species, $(S–1)^{-1}$ is equal to 1, so the denominator of the FRO is 0 and the index is not defined. For assemblages with more than 2 species, but with only 2 trophic levels (i.e. some species have the same value of trophic level), there is only 1 PEW different from 0 and it is equal to 1 so that:

$$\sum_{l=1}^{S-1} \min\left(PEW_l, \frac{1}{S-1}\right) = \frac{1}{S-1} \qquad (5)$$

and FRO is always 0.

The relationship between each of the 4 trophic diversity indices and abiotic parameters was estimated using a Bayesian model selection procedure for multiple linear regressions (function ‘bicreg’ of the BMA package under R software). This method is a Bayesian-based approach that quantifies the relative support of various models in the data (Johnson & Omland 2004). The selection procedure was conducted using the BIC (Bayesian information criterion), and the inclusion of models in the final set was based on the analysis of Bayes factor (ratio of a model’s posterior probabilities interpreted as the likelihood of one model versus another given the observed dataset; Burnham & Anderson 2002).

A hierarchical classification using the Ward method (R package cluster) was carried out to classify the 37 stations into zones according to the values of 10 environmental parameters for the 12 mo of the present study. According to previous studies (Ramos Miranda et al. 2005a), 3 seasons were defined based on weather conditions (wind, rain and temperature): the dry season (February to May), the wet season (June to September) and the 'Nortes' season (October to January).

Analyses of variance (ANOVA) with 2 factors (zone, season and their interaction) were computed using the 4 trophic diversity indices (Table 1) and species richness as predicted variables.

For each pair of stations, we estimated dissimilarity between the 2 assemblages by using the Bray-Curtis index. We chose this index because it measures the 2 facets of biotic dissimilarity: species identity and species dominance.

Similarly for each pair of stations (i,j) and for each trophic diversity index and species richness (Ind_k), we computed the distance $\mathrm{dInd}_k(i,j)$ to estimate the absolute relative difference in index values with:

$$\mathrm{dInd}_k(i,j) = \frac{[2 \times \|\mathrm{Ind}_k(i) - \mathrm{Ind}_k(j)\|]}{[\mathrm{Ind}_k(i) + \mathrm{Ind}_k(j)]} \qquad (6)$$

Then, to test whether the biotic dissimilarity between 2 assemblages correlates with the dissimilarity of their trophic diversity, 6 Mantel's tests were computed (package 'ape' of R software) between the Bray-Curtis dissimilarity matrix and each of the matrices containing a diversity dissimilarity (richness and 4 trophic diversity indices).

Given the geographical zones discriminated by the Ward classification and the a priori fixed seasons, we aggregated data for species abundance from corresponding stations into spatiotemporal strata. Species richness and trophic diversity indices were also estimated for each stratum. We then applied the same methodology as at the local scale to discover whether the dissimilarity in trophic diversity indices is related to the dissimilarity in species composition.

RESULTS

Among the 444 sampling points (37 stations × 12 mo), 132 were removed before statistical analysis because (1) environmental parameters were missing after technical problems (96 sampling points), or (2) the net was empty (11 sampling points), (3) we caught fewer than 3 different trophic levels which is the minimum needed to compute trophic diversity indices (28 sampling points).

In the 312 remaining samples, a total of 36744 nektonic organisms were caught for a total biomass of ~600 kg.

Total species richness was of 101 species: 83 teleosts, 5 elasmobranchs, 7 shrimp species (family Penaeidae), 4 crab species (genus Callinectes), 1 Mantis shrimp (Squilla empusa) and 1 squid (Lolliguncula brevis). Invertebrates (mainly shrimps and crabs) were often an important part of the biomass (mean ± SD: 32.9 ± 27.6%). Their contribution to the total biomass of each nekton assemblage ranged from 0 to 100%.

Environmental parameters

As expected, environmental variables showed large ranges of values. Water depth varied from 0.8 to 12.4 m with a mean ± SD of 4.2 ± 2.5 m. Transparency values filled all the potential range (varying from 2 to 100%), but the mean remained low (15.7 ± 14.7%). Similarly, surface salinity ranged from 0.2 to 40.5 PSU (mean 28 ± 9.7 ppm) showing a gradient from euhaline to freshwater conditions. Water temperature was high (27.8 ± 2.6°C) with extreme values of 22.5 and 32.5°C during the Nortes season and at the end of the dry season, respectively. The pH showed a large range of values from 5.05 to 8.94 (7.74 ± 0.72). Dissolved oxygen values varied from 1.5 to 9.8 mg l^{-1} with a mean value of 6.4 ± 1.5 mg l^{-1}.

As expected, given the low depth, physico-chemical parameters measured at the surface and at the bottom of the water column were highly correlated (0.949 for temperature, 0.860 for salinity, 0.966 for pH and 0.834 for dissolved oxygen). Furthermore, some environmental parameters were significantly correlated with one another, but Pearson coefficients of correlation remained low (<0.57). For example, depth and salinity were positively correlated ($r = 0.509$ for surface water and $r = 0.555$ for bottom waters). Temperature and dissolved oxygen were globally negatively linked with a coefficient of correlation ranging from –0.466 to –0.569 for surface and bottom waters, respectively.

The hierarchical classification, based on environmental conditions, discriminated 3 main clusters (Fig. 3): one group (Coast 1) with Stns 1 to 12 corresponding to the coast between the mouth of the Usumacinta River and the mouth of the San Pablo y Pedro River (Fig. 1); a second group (Coast 2) with Stns 13 to 25 corresponding to the external edge of the Terminos lagoon; and a third group (Lagoon) with Stns 26 to 37 located in the southern part of the lagoon. In other words this classification based on environmental parameters matches the geography of the coast (Fig. 1).

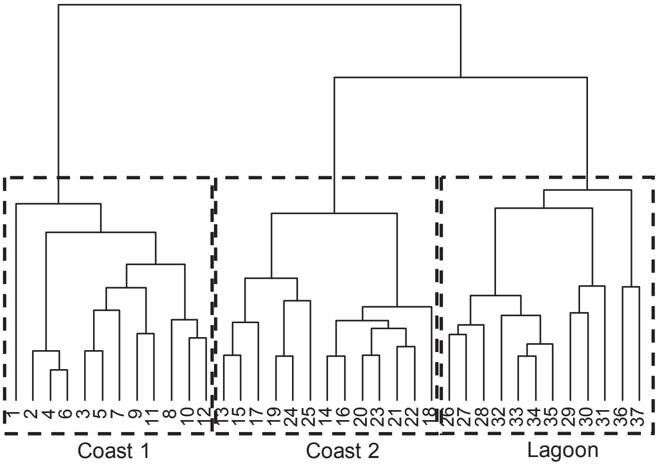

Fig. 3. Dendrogram of the 37 stations according to a Ward's classification based on 10 environmental parameters measured each month. Three zones corresponding to the 3 main clusters were named based on their position on the transect (Fig. 1)

Environmental effects on trophic diversity indices

Given the very strong correlations between physico-chemical measures at the 2 layers (surface and bottom) of the water column, we used only bottom temperatures, salinities, pH and dissolved oxygen values for multiple regressions. Table 1 shows the results of the Bayesian model selection procedure carried out for the modeling of the 4 trophic diversity indices as a function of depth, transparency, bottom temperatures, salinities, pH and dissolved oxygen values. Very similar results were obtained using surface physico-chemical variables, but we do not present them for reasons of clarity. For each of the 4 indices, the evidence of the best model over the second-best (given by the Bayes factor) was always substantial, thus only 1 model was retained during the selection.

Table 1. Results of a Bayesian model selection procedure for linear model regressions carried out using trophic diversity indices as explained variables and 6 environmental parameters as explanatory variables for 312 sampling points. Only the variables retained by the models are presented. For each trophic diversity index, only one model was retained by the selection procedure. For this model, the coefficient posterior expected values for the explanatory variables, the R^2 and Bayes factor (evidence of the best selected model versus the second-best) are presented. FD_{var} = FD_{var} index of Mason et al. (2003); FRO = functional regularity index. –: variables not selected in the final model

	Depth	Trans-parency	Bottom temp.	R^2	Bayes
No. of trophic levels	–0.412	–	0.376	0.145	7.29
Range of trophic levels	–	–	0.033	0.038	1.48
FD_{var}	0.007	0.080	–	0.157	3.83
FRO	0.012	–	–	0.039	5.76

Only 3 out of 6 variables had an effect on the 4 indices: depth, transparency and bottom temperature. Furthermore, for each index, few environmental variables explained trophic diversity index variations. Water depth negatively influenced the number of trophic levels. The trophic range and the number of trophic levels were positively affected by the bottom temperature. Trophic divergence index was positively related to water depth and transparency. Only water depth influenced trophic evenness.

Overall, the linear models explained only between 3.8 and 15.7% of the total variation of nekton trophic diversity indices.

Testing spatial and temporal effects on trophic diversity

Table 2 shows the results of the ANOVAs carried out at the local scale (station). Spatial effect significantly influenced species richness and the number of trophic levels, with more species collected in stations within the lagoon than in stations situated outside. FD_{var} varied significantly with the zone while the interaction between season and zone factors was significant. The 2 other indices (range and FRO) were unaffected by the 2 factors or by their interaction. Fig. 4 clearly shows the spatiotemporal consistency for these latter indices.

Relations between species turnover and trophic diversity dissimilarities

At the local scale (station), the mean ±SD Bray-Curtis dissimilarity index was 0.853 ± 0.147 between samples.

The Mantel tests showed positive significant correlations between Bray-Curtis dissimilarities and each of the 5 absolute relative differences for indices but with low Mantel correlation coefficients (0.21 for species richness and <0.22 for the 4 trophic diversity indices). This outcome means that even if the similarity between 2 communities significantly affects the similarity of their trophic structure, the effect remains weak.

With the 3 seasons and 3 geographical zones, 9 spatiotemporal strata were constructed from the 312 stations. At this regional scale the Bray-Curtis dissimilarity among strata dropped to 0.493 ± 0.101. For all trophic diversity indices, the Mantel tests showed no significant relationships between the

Table 2. ANOVA F-values for the effect of spatial and temporal factors on 4 trophic diversity indices and species richness for 312 sampling points. The degree of freedom (df) of each factor is given at the head of the column. FD_{var} = FD_{var} index of Mason et al. (2003); FRO = functional regularity index. ^{ns}non significant; *p < 0.05; **p < 0.01; ***p < 0.001

Index	Season (df = 2)	Zone (df = 2)	Zone × Season (df = 4)
No. of species	0.996^{ns}	6.348**	2.147^{ns}
No. of trophic levels	2.501^{ns}	10.585***	2.049^{ns}
Range of trophic levels	1.394^{ns}	1.936^{ns}	1.287^{ns}
FD_{var}	1.612^{ns}	3.437*	2.949*
FRO	1.951^{ns}	0.028^{ns}	0.415^{ns}

indices and the species turnover in nekton species assemblages. As an illustration, Fig. 5 presents the trophic spectrum of the 9 spatiotemporal strata (regional scale), showing a global consistency for all indices despite species turnover, particularly between stations belonging to the wet and Nortes seasons.

DISCUSSION

Environmental conditions were highly variable in space and time among our sampling points, as expected from the freshwater influence in this coastal area. Indeed, environmental conditions range from freshwater (near the mouth of the streams) to marine water (near the northern part of Carmen Island) with many intermediate states in terms of salinity, transparency and water depth (from the inner lagoon to the adjacent coast). More generally, the whole area could be divided into 3 main zones according to environmental conditions, and these 3 zones are consistent with the global hydrology (influence of the streams, current flowing thought the lagoon and marine water entries) (Figs. 1 & 3). In parallel, the nekton composition in terms of species abundances is also highly different among samples (Bray-Curtis ranging from 0.082 to 1) and among spatiotemporal strata (Bray-Curtis ranging from 0.234 to 0.666), highlighting the high species turnover in these estuarine environments (e.g. Wagner 1999). The present case study is thus ideal to seek potentially stable patterns in trophic structure because tropical estuarine ecosystems contain many species and are characterized by high variability for both biotic and abiotic variables.

The multiple regressions with environmental variables (Table 1) showed that only a few environmental parameters drive the trophic structure of nekton assemblages. Trophic richness is mainly influenced by depth and temperature. Divergence is affected by depth and transparency and evenness just by depth. However, and this is the key point, the overall weak predictive power of the multiple regressions (3.8 to 15.7%) suggests that the trophic diversity of nekton assemblages is relatively stable along environmental gradients.

This result is confirmed by ANOVA tests showing that trophic range and trophic evenness are invariant across space and time (Fig. 4), while species richness and the number of trophic levels differ among zones. The findings suggest that even when changes occur in nektonic species richness, trophic diversity indices remain stable over space and time. More generally, Bray-Curtis dissimilarities between pairs of samples demonstrate the high turnover in the composition of nekton assemblages. The significant but weak correlations observed at the local scale between these assemblage dissimilarities and differences observed for trophic diversity indices do not

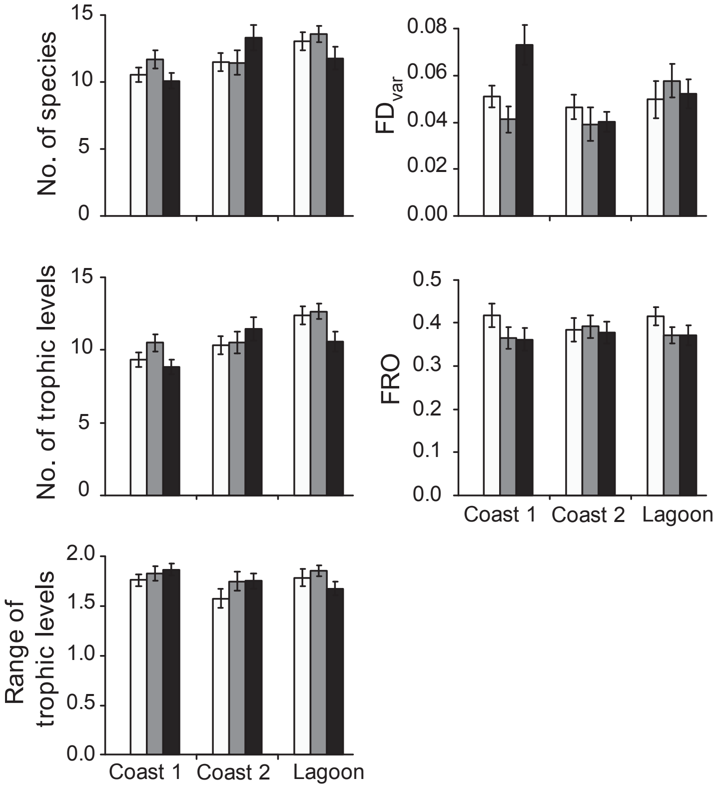

Fig. 4. Mean (±SE) of species richness and of 4 trophic diversity indices estimated over areas (see Figs. 1 & 3) and seasons. 'Dry' (white bars) corresponds to the period from February to May, 'wet' (grey bars) to June to September and 'Nortes' (black bars) to October to January. ANOVA tests are summarized in Table 2. FD_{var} = FD_{var} index of Mason et al. (2003); FRO = functional regularity index

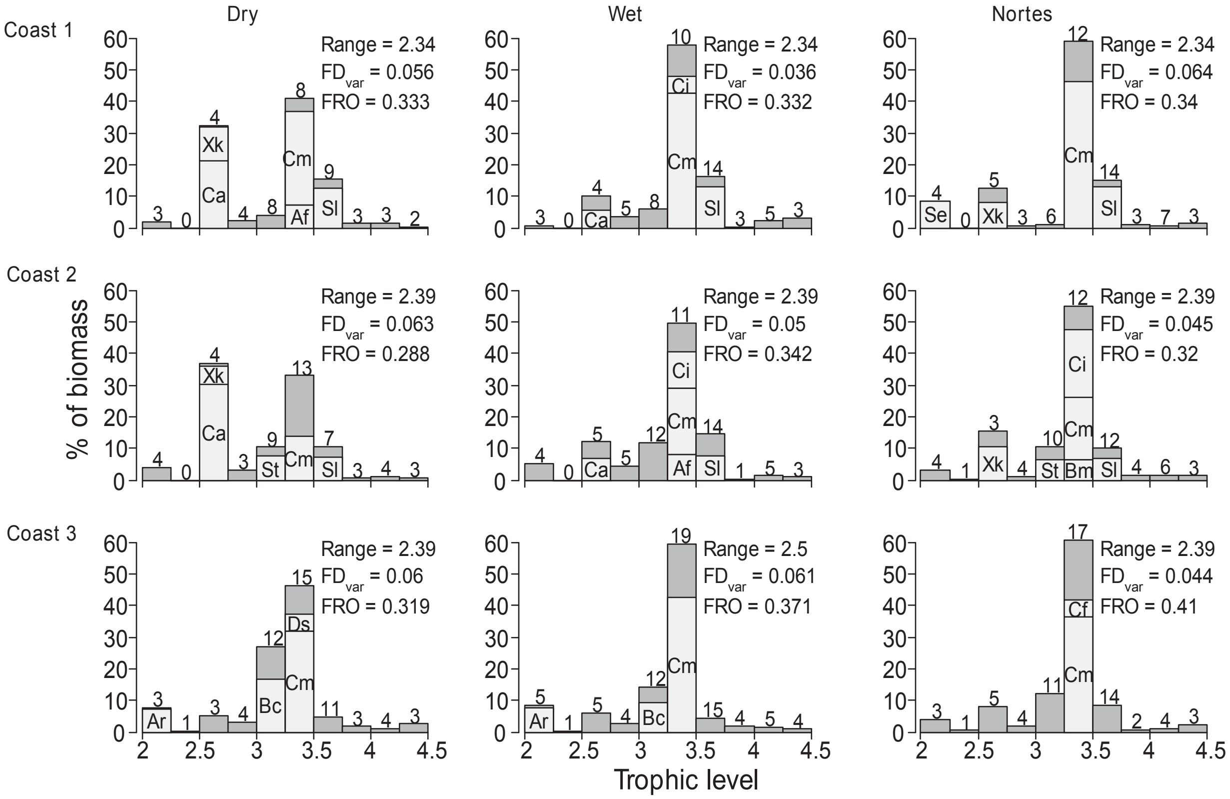

Fig. 5. Biomass distribution along the trophic level (TL) axis for each of the 9 spatiotemporal strata. Ten classes of TL were considered (each class has a width of 0.25). The values of the 3 trophic diversity indices are given for each stratum. For each class, the number of species is given at the top of the corresponding bar. The relative biomasses >5% are represented by white rectangles, with the coded names of the species inside: Ariopsis felis (Af), Archosargus rhomboidalis (Ar), Bagre marinus (Bm), Bairdiella chrysoura (Bc), Callinectes sapidus (Ca), Callinectes similis (Ci), Cathorops melanopus (Cm), Chaetodipteurs faber (Cf), Dasyatis sabina (Ds), Sphoeroides testudineus (St), Squilla empusa (Se), Stellifer lanceolatus (Sl) and Xiphopenaeus kroyeri (Xk)

arise simply from strong similarities in assemblage compositions. In other words, although species composition differs among local assemblages, the trophic structure of nekton assemblages is rather similar.

In particular, the high species turnover holds also for dominant species (Table 3). Indeed, 14 different species were ranked among the top 3 in terms of biomass for more than 5% of the stations. Among these 14 species, 4 taxonomic groups of the 6 present at the regional scale were represented (Teleostii and 3 crustacean families: Penaeidae, Squillidae and Portunidae). Therefore, we can reject the hypothesis that our stable patterns at the local scale for trophic divergence and evenness result from the presence of a couple of ubiquitous and abundant species that may homogenize the trophic structure of nekton assemblages regardless of environment. For instance, the most abundant species over all the samples, the dark sea catfish Cathorops melanopus, was present in 60% of the stations but was among the 3 most abundant species in only 75% of these cases, or just 45% of the 312 stations. Conversely, the American stardrum Stellifer lanceolatus was the most widespread species, present in 71% of the stations, but among the 3 dominant species in only 28% of the cases. The Western Atlantic seabream Archosargus rhomboidalis was globally scarce but was quite abundant when present.

Moreover, because all abundant species, except the Western Atlantic seabream and the mantis shrimp Squilla empusa, have relatively similar trophic levels (between 2.6 and 3.5); the biomass of nekton assemblages tended to peak at 3 in all the samples despite high species turnover. As a consequence, trophic evenness and trophic divergence indices, which describe the distribution of biomass along the trophic axis, tended to show stable patterns at the local scale (Fig. 4) with weak relationships to environmental variables.

Species turnover is also remarkable for the 2 extremities of the trophic chain (Table 4). For the minimum trophic level, 7 species (with trophic levels less than 2.7) contributed to 96% of the cases. As a result, in 64% of the stations studied, the minimum trophic level was consistently low (less than 2.3). Similarly, 4 species

Table 3. List of dominant species for trophic diversity patterns at the local scale (i.e. over the 312 sampling points). Main taxonomic groups are given in parentheses: Fi = Fish (Teleosteii), Cr = Crab (Portunidae), Sh = Shrimp (Penaeidae), and Msh = Mantis shrimp (Squillidae). The percentage of occurrence is the proportion of stations in which the species was present. The values in the 4 last columns are the percentages of stations where the species was, respectively: the most abundant species (in terms of biomass), the second-most abundant, the third-most abundant and, finally, where it was among the 3 dominant species

Taxon	Trophic level	% occurrence	% 1st	% 2nd	% 3rd	% (1st, 2nd, or 3rd)
Cathorops melanopus (Fi)	3.35	58.97	28.85	9.94	6.09	44.88
Callinectes sapidus (Cr)	2.6	43.27	13.14	6.73	7.69	27.56
Callinectes similis (Cr)	3.3	46.47	9.94	6.41	7.05	23.40
Xiphopenaeus kroyeri (Sh)	2.7	58.97	9.62	8.01	8.33	25.96
Stellifer lanceolatus (Fi)	3.5	71.15	6.41	12.82	9.62	28.85
Bairdiella chrysoura (Fi)	3.2	33.33	4.81	4.17	2.24	11.22
Archosargus rhomboidalis (Fi)	2.22	12.82	3.53	3.85	2.88	10.26
Bagre marinus (Fi)	3.28	45.19	2.88	5.13	3.85	11.86
Ariopsis felis (Fi)	3.29	34.29	2.56	5.45	5.45	13.46
Squilla empusa (Msh)	2.2	35.90	2.24	4.17	2.56	8.97
Sphoeroides testudineus (Fi)	3.24	22.76	2.24	4.49	3.85	10.58
Chaetodipterus faber (Fi)	3.39	19.23	1.92	2.24	2.24	6.40
Symphurus plagiusa (Fi)	2.99	45.19	1.60	2.56	4.49	8.65
Litopenaeus setiferus (Sh)	2.7	50.64	0.32	2.88	2.56	5.76
		Total	90.06	78.85	68.90	

contributed to 64% of the maximum trophic level observed (16 for 90%), with trophic levels greater than 4. As a consequence, locally, the trophic range was very consistent across space and time, ca. 1.7 to 1.8, regardless of species composition and environmental conditions. In addition, some species with low (the crab Callinectes sapidus and the shrimp Xiphopenaeus kroyeri) or high trophic levels (the fishes Cynoscion arenarius and Cynoscion nothus) were ubiquitous enough to prevent the decrease of trophic chain length in all sampled assemblages. Indeed, these 4 species did not have the most extreme TL values (the 2 low TL values were ~2.6 and the 2 high TL values were ~4.1), but when the species with the most extreme trophic level values were absent, these 4 widespread species prevented the trophic range from decreasing too much and played an insurance role in maintaining the trophic chain length. Thus, despite a high species turnover among nekton assemblages, we observed a stable trophic chain length attributable to a species replacement for either low or high trophic values or to the presence of some abundant and widespread species at the regional scale with both low and high trophic levels.

Compared to the local scale, the patterns that emerged at the regional scale were even more remarkable (Fig. 5). The histograms in Fig. 5 confirm the regional predominance of species with trophic levels ~3.25: the class 3.25 to 3.5 consistently accounted for more than half of the total nekton biomass. More precisely, for all the strata belonging to the wet and Nortes seasons, the trophic class 3.25 to 3.5 accounted invariably for between 50 and 60% of the total biomass (in 5 cases out of 6, the value is very close to 60%), which is not a trivial result. At this regional scale of observation, the contribution of the most abundant species Cathorops melanopus to the total biomass ranges from 14 to 46%. Therefore, the peak of biomass between 3.25 and 3.5 was not always and solely due to the dark sea catfish but also to the swimming blue crab Callinectes similis (TL = 3.3) and to the hardhead sea catfish Ariopsis felis (TL = 3.29), with respective maxi-

Table 4. Species within extreme trophic levels as well as their occurrences and their percentages of presence at the most extreme trophic level in assemblages. Main taxonomic groups are given in parentheses: Fi = Fish (Teleosteii), Cr = Crab (Portunidae), Sh = Shrimp (Penaeidae), and Msh = Mantis shrimp (Squillidae)

Taxon	Trophic level	% occurrence	% min or % max
Minimum trophic levels			
Squilla empusa (Msh)	2.2	35.90	26.60
Callinectes sapidus (Cr)	2.6	43.27	18.27
Cetengraulis edentulus (Fi)	2.11	17.31	17.31
Sicyonia brevirostris (Sh)	2.2	12.82	10.58
Archosargus rhomboidalis (Fi)	2.22	12.82	9.62
Litopenaeus setiferus (Sh)	2.7	50.64	9.62
Xiphopenaeus kroyeri (Sh)	2.7	58.97	3.85
Total			95.85
Maximum trophic levels			
Cynoscion arenarius (Fi)	4.28	37.18	24.68
Trichiurus lepturus (Fi)	4.45	19.87	18.91
Cynoscion nothus (Fi)	4.04	27.56	10.58
Synodus foetens (Fi)	4.5	8.97	8.97
Total			63.14

mum contributions of 20 and 8%. Moreover, besides these dominant species, a lot of other species (8 to 19) contributed to the peak between 3.25 and 3.5.

Overall, the results obtained at the regional scale among the 9 spatiotemporal strata showed that variations in trophic diversity indices do not correlate with the rate of species turnover in nekton assemblages. For example, Nortes Coast 1 and Wet Coast 2 had a Bray-Curtis index of 0.575, but exhibited low differences in their trophic divergence and trophic evenness (Fig. 5). In other words, 2 very different assemblages (in terms of species composition and/or abundance) are as likely to have similar patterns of trophic diversity as are 2 assemblages with similar specific composition. These results suggest again that despite variations in species composition and abundances among strata, we observed a remarkably stable pattern in the trophic structure of nekton assemblages.

The composition of nektonic assemblages supports the need for taking into account all organisms without taxonomic considerations. Indeed, if we just consider fish, we have a bias in the nekton trophic diversity estimation because shrimps and crabs are abundant in this area and have low trophic levels compared to most fish species. For example, among the 12 lowest trophic levels, only 5 corresponded to fish species; among these, only 3 were abundant species. If shrimps and crabs had not been captured or considered in the present study, the base of the trophic chain would have been partially reduced and our conclusions about stable trophic structures would thus have been biased. For example, the swimming blue crab Callinectes sapidus and the shrimp Xiphopenaeus kroyeri constitute most of the biomass for the trophic class between 2.5 and 2.75, which drives the trophic structure, especially for the 2 coastal zones during the dry season (Fig. 5).

The sampling method using a shrimp trawl is probably the best for estimating nekton trophic diversity because it is an active method and because the small mesh size allows capturing both fish and small invertebrates.

A limitation in the present study comes from the estimation of the trophic level. Coastal areas and more particularly coastal lagoons are marked by the presence of age classes from juveniles to adults, depending on species' reproductive strategies. Diet can change with growth, and even if the corresponding trophic levels are known, it is difficult to associate them correctly with each individual. Because the trophic level increases with body size for high trophic level species, we certainly overestimated the trophic level for small individuals of species at high trophic levels (such as Cynoscion sp.). Furthermore, in highly variable systems such as coastal zones, the diet of omnivorous macroorganisms is not homogeneous throughout the year, but follows migrations and seasons. In our data set, some species have similar values for trophic level: in total we had 101 species but only 66 different trophic level values. Because trophic level is a continuous trait ranging from 2 to 4.5 for heterotrophic organisms, the number of entities would be a priori synonymous with species richness. However, estimated trophic levels from the literature are sometimes provided at the level of the genus, with related species then being assigned the same trophic level value. This bias is not inherent in the trophic level concept but instead arises from the lack of data, underlining the difficulty of developing a large and complete database of many species for functional traits. Finally, despite these intrinsic and extrinsic biases due to the trophic level estimation, we still consider that this ecological trait has the advantage of providing a good approximation of the position of all nekton species along the trophic chain without any taxonomic limitation.

Many studies dealing with trophic interactions in aquatic systems elucidate 2 structuring forces (Leibold et al. 1997, Maciej Gliwicz 2002). When the amount of nutrient is the limiting factor, a bottom-up effect constrains the reproduction and growth of the lowest trophic levels and then limits the abundance of their predators (Ware & Thomson 2005, Frederiksen et al. 2006). The maximum biomasses are thus at the lowest trophic levels. Conversely, when top predators are abundant they may have a top-down effect on their preys which themselves prey on species of lower trophic levels. The biomasses of species belonging to low trophic levels are under the control of the species within the highest trophic levels. In the present case study, none of these effects appeared to occur: we observed stable trophic structures centered around the middle of the trophic axis through space and time and along environmental gradients. Indeed, on the one hand, the 3 main streams carry a lot of organic matter and nutrients throughout the year and especially during the wet season when the freshwater discharge is high. This continuous flow may not limit the primary productivity and primary consumption in the ecosystem and thus may prevent the trophic structure from experiencing a bottom-up effect. On the other hand, as described previously, top predators (i.e. species with trophic levels higher than 4.0) are not as abundant in biomass compared to the potential biomass of preys, whatever the season or zone, and thus are unlikely to provoke a top-down effect. Humans, through fishery activities, may also modify trophic structure in species assemblages (Pauly et al. 1998). The only fishery in the Terminos Lagoon area is shrimp, primarily around the city of Ciudad del Carmen. The nets used are like the one we used for sampling. As explained previously, these small mesh nets are nonselective, and there are high quantities of bycatch (crabs and fishes). Therefore, we suppose that fishing similarly decreases the biomasses of all trophic levels and thus may not deeply modify the trophic structure of nekton assemblages.

We have found advantages to describing trophic diversity based on a set of indices that focuses on each of its 3 independent components; indeed, our indices summarized the shape of the Biomass Trophic Level Spectra proposed by Sosa-López et al. (2005). Using this promising approach, we have shown that the nekton assemblage trophic structure along the Terminos coast is unexpectedly stable despite strong environmental gradients that enhance species turnover in space and time. In turn, these results suggest that some deterministic ecological processes may shape the trophic structure of food webs, at least in nektonic coastal assemblages. A comparison with similar systems is now needed to confirm the relative invariance of trophic diversity along environmental gradients in estuarine ecosystems. Our results also show that researchers gain to consider all the organisms when seeking stable trophic patterns in assemblages because taxonomically different species may occupy the same trophic level and have the same impact on the food web. Such integrative approaches are implemented in Ecopath models to explore how biotic groups transfer matter through the ecosystem (e.g. Cruz-Escalona et al. 2007). The outputs of such models would contribute to the understanding of mechanisms underlying emergent properties of trophic structures.

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Chapitre 6

Perte de diversité fonctionnelle face aux changements environnementaux entre 1980 et 1998

6.1 Dégradation des habitats et perte d’espèces : quels impacts sur la diversité fonctionnelle ?

Les changements globaux affectent les êtres vivants et modifient notamment les assemblages d’espèces localement et régionalement (Sala *et al.* 2000). En particulier, les changements des conditions environnementales et plus largement des habitats entraînent des changements d’aires de distribution voire l’extinction de certaines espèces (Thuiller *et al.* 2005). Ces changements dans la composition et la structure des communautés sont particulièrement bien étudiés en terme de diversité spécifique. Le nombre d’espèces est en effet un bon indicateur pour estimer les taux d’extinction, la diversité des habitats et donc leur état de dégradation, ou la valeur d’un écosystème en terme de conservation (point « chauds » de biodiversité).

Cette approche est aussi sous-tendue par l’hypothèse que plus le nombre d’espèces est grand, meilleurs seront les services écosystémiques fournis aux populations humaines (Diaz *et al.* 2007). Or, de nombreuses études ont montré que la diversité fonctionnelle influençait plus fortement les processus écosystémiques que la richesse spécifique (Petchey 2004). L’effet de la richesse spécifique est donc indirect, sous l’hypothèse que plus il y a d’espèces, plus grande est la probabilité d’avoir de nombreuses fonctions assurées dans le système. Parallèlement, plus il y a d’espèces, plus la redondance pour chaque fonction est forte et par conséquent plus faible est la probabilité de perdre une fonction en cas d’extinction. Néanmoins ces hypothèses ne sont pas toujours vérifiées, par exemple lorsque certaines fonctions ne sont assurées que par une seule espèce ou plus généralement du fait que ce sont souvent les quelques espèces les plus abondantes qui influencent les processus écosystémiques. En définitive, il apparaît donc plus direct de mesurer l’effet des changements globaux sur la diversité fonctionnelle. Il est à noter qu’à notre connaissance, ceci reste très peu étudié (mais voir l’intéressante étude de Ernst *et al.* (2006), sur l’effet des exploitations forestières sur les communautés de grenouilles tropicales).

Face aux changements environnementaux et à la perte d’espèces consécutive, la question en suspens est donc : comment la diversité fonctionnelle est elle affectée ? Elle peut être conservée grâce à la redondance fonctionnelle entre espèces, autrement dit si les espèces perdues ne représentaient pas des types fonctionnels uniques. Au contraire, elle peut subir elle aussi une forte diminution, si la perte d’espèces entraîne la perte de certaines fonctions.

6.2 La lagune de Terminos : un écosystème sous contraintes

Ramos-Miranda *et al.* (2005) et Sosa-López (2005) ont mis en évidence un certain nombre de changements majeurs survenus dans la lagune de Terminos entre les années 1980 et 1998. D’un point de vue physico-chimique la lagune s’est fortement comblée avec une diminution de la profondeur d’en moyenne un mètre. Ce comblement s’est notamment accompagné d’une diminution des herbiers de phanérogames présents dans la partie nord. Par ailleurs, les communautés de poissons ont été fortement affectées, avec des changements dans leur composition et plus particulièrement un remplacement dans l’identité des espèces dominantes. De plus, les nouvelles espèces occupant la lagune sont taxinomiquement proches de celles déjà présentes alors qu’au contraire les espèces ayant disparu étaient les seules représentantes de certains clades. Au vu de ces résultats, il nous a semblé indispensable d’aller plus loin que cette approche taxinomique et de tenir compte de l’identité fonctionnelle des espèces.

6.3 Qu’avons-nous perdu à Terminos en 18 années : des espèces ou des fonctions ?

Nous avons ainsi caractérisé les changements de diversité fonctionnelle survenus dans la lagune de Terminos entre 1980 et 1998 (Manuscrit H, Villéger *et al.*, soumis à *Ecology*) . Pour cela nous avons utilisé les données d’abondances récoltées sur les 18 stations et les traits mesurés pour les deux fonctions. Nous avons considéré quatre zones environnementales, définies d’après les conditions observées en 1980. Pour chacune de ces zones, nous avons calculé les trois composantes de la diversité fonctionnelle grâce aux indices proposés dans le Manuscrit B ainsi que le degré de spécialisation des communautés en suivant la méthode proposée par Bellwood *et al.* (2006b).

Pour chacun de ces indices, les changements observés entre les deux périodes ont été testés par un modèle nul, l’hypothèse H0 étant l’absence de différence entre les années 80 et 98. Les résultats montrent que la zone le long de l’île de Carmen est la plus riche en espèces et contient plus de la moitié de la biomasse piscicole de la lagune. Néanmoins, la biomasse de cette zone a diminué de moitié en 18 ans, alors que la richesse spécifique a fortement augmenté passant de 56 à 76 espèces. Du point de vue de la structure fonctionnelle des communautés de poissons, cette zone voit par contre sa divergence et sa spécialisation fonctionnelles diminuer significativement pour les deux fonctions étudiées. Cette perte de diversité fonctionnelle est due à un fort remaniement des espèces dominantes. En effet, deux espèces typiquement inféodées aux herbiers et initialement dominantes ont vu leurs abondances diminuer fortement. Dans le même temps deux espèces pélagiques et détritivores, présentes marginalement dans cette zone en 1980 sont devenues dominantes. Or, les deux espèces « perdantes » présentaient des combinaisons de traits originales en terme d'acquisition de la nourriture (en relation avec leur régime composé d'épiphytes et de coquillages) et de locomotion (bonne manoeuvrabilité) alors que les deux espèces « gagnantes » présentent des fonctions semblables à celles des espèces déjà présentes. D'un point de vue écosystémique, le facteur déterminant de cette perturbation majeure est la perte des herbiers. Cette dernière est probablement due au comblement et aux pollutions d'origines anthropiques consécutives au développement urbain et industriel de l'île de Carmen. La mise en évidence d'une diminution de la diversité fonctionnelle alors que la richesse spécifique a augmenté souligne la pertinence de l'approche multi-facettes de la diversité fonctionnelle pour caractériser l'impact des changements globaux sur les communautés.

Par ailleurs, ce résultat paradoxal souligne la nécessité d'étudier plus en détail l'impact des changements globaux, même lorsque les indicateurs tels que la richesse spécifique n'indiquent pas de perturbation. En effet, le fonctionnement et la stabilité des écosystèmes sont souvent déterminés par quelques espèces jouant un rôle clé (Bellwood *et al.* 2003) parfois même de manière cryptique (cf Bellwood *et al.* 2006a et la notion de groupe fonctionnel dormant).

MANUSCRIT H

Losing functional diversity while species richness increases: a biodiversity paradox in fish communities

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Abstract

Human activities have strong impacts on ecosystem functioning through their effect on abiotic factors and on biodiversity. There is also growing evidence that species functional traits link changes in species composition and shifts in ecosystem processes. Hence, it appears to be of utmost importance to quantify modifications in the functional structure of species communities after human disturbance. Despite this fact, there is still little consensus on the actual impacts of human-mediated habitat alteration on the components of biodiversity which include species functional traits. Therefore, we studied changes in taxonomic diversity, in functional diversity and in functional specialization of estuarine fish communities facing drastic environmental and habitat alterations. The Terminos lagoon (Gulf of Mexico) is a tropical estuary of primary concern for its biodiversity, its habitats and its resource supply, which has been severely impacted by human activities. Fish communities were sampled in four zones of the Terminos lagoon 18 years apart (1980 and 1998). Two functions performed by fish (food acquisition and locomotion) were studied through the measurement of 16 functional traits on more than 1000 individuals belonging to 62 species. Functional diversity of fish communities was quantified using three independent components: richness (functional space occupied by the community), evenness (regularity in the distribution of species abundances in the functional space) and divergence (how species abundances diverge from the center of the functional space). Additionally, we measured the degree of functional specialization in fish communities. We used a null model to compare the functional structure of fish communities between 1980 and 1998. Surprisingly, in the northern part of the lagoon, we found an increase of fish richness but a significant decrease of functional divergence and functional specialization. We explain this result by a decline of specialized species, i.e. those with particular combinations of traits, while new occurring species are redundant with those already present. The species that decreased in abundance have functional traits linked to seagrass habitats which regressed consecutively to increasing eutrophication. The paradox found in our study highlights the need of a multifaceted approach in the assessment of biodiversity changes in communities under pressure.

Key words: fish ecomorphology, eutrophication, environmental changes, functional richness, functional evenness, functional divergence, estuarine ecosystem, Terminos lagoon, seagrass beds

Introduction

Global environmental changes are increasingly affecting all ecosystems including the good and services they provide for human societies. Anthropogenic impacts are deeply modifying – sometimes irreversibly - environments through climate warning and geochemical flux disturbances (Vitousek et al. 1997). Ecological communities are also strongly impacted through habitat loss, introduction of species and resource depletion (hunting, fishing), and it is now widely accepted that we are facing the sixth extinction crisis (e.g. for bony fishes 800 species endangered or vulnerable out of 1,721 evaluated, Baillie et al. 2004). More generally, the loss of biodiversity is a critical issue for both conservation purposes and sustainability of ecosystem services (Constanza et al. 1997, Diaz et al. 2007). Nowadays, biodiversity changes have been widely reported, and evidence linking the diversity of communities and ecosystem processes is constantly growing (see Hooper et al. (2005) for a review). Thus, we urgently need to determine the factors that maintain or threaten the biodiversity of communities.

Classically, biodiversity changes have been assessed using diversity indices among which the most commonly used is the number of species also called species richness. However, abundance patterns in species communities are also responsible for many ecosystem processes (see Hillebrand et al. (2008) for a review). For instance, the level of dominance in communities determines the resistance against invasion (Emery and Gross 2006) and regulates species richness-decomposition relationships (Dangles and Malmqvist 2004). However, the indices that take into account the evenness of abundance distribution among species (e.g. Shannon-Wiener) and describe more precisely community structure still provide an incomplete view of biodiversity. Indeed, they do not yet consider the identity of species and biological differences among species. However, recent consensus points out the importance of particular taxon rather than species richness *per se* to explain ecosystem processes in plant (Johnson et al. 2008), animal (Valone and Schutzenhofer 2007) or aquatic communities (O'Connor et al. 2008).

A step further in biodiversity assessment needs to consider the role of each species in ecosystems or species responses to environmental conditions. Let us consider two communities with five fish species each. The first one contains anchovy, jack, moray, flatfish and butterfly fish while the second one contains five butterfly fish species. Species richness has a value of five for both communities but biological diversity in terms of morphology, diet, swimming ability and life-history traits is clearly greater in the former community. This is actually what the functional view of biotic communities aims to quantify (McGill et al. 2006). However, there is still no consensus on the actual impacts of habitat alteration on different aspects of biodiversity including functional diversity, even if Ernst et al. (2006) reported a dramatic loss of functional diversity in tropical amphibian communities after selective logging. Thus, the question is no longer whether anthropogenic impacts modify the biodiversity of communities but (*i*) which facet of biodiversity is mostly affected, (*ii*) are functional diversity and species richness declining in parallel, and (*iii*) can we mechanistically relate a loss of functional diversity to habitat degradation? Here, through the use of novel estimators designed to measure functional diversity within a multifaceted and multidimensional framework, we studied the modifications in the structure of coastal fish communities after 18 years and a degradation of habitats.

Functional ecology is based on the use of functional traits which are defined as biological attributes that influence organismal performances (Violle et al. 2007). Basically, functional traits have to be related to ecosystem processes (effects traits) or to ecosystem stability through resistance and resilience (response traits). The use of functional traits, independently from taxonomy, aims to develop a functional approach of community ecology (McGill et al. 2006). A step beyond species richness, functional diversity has soon appeared as a powerful tool to link community composition to ecosystem properties (Tilman et al. 1997) and then to ecosystem services (Diaz et al. 2007). For instance, numerous studies have highlighted relations between functional diversity and ecosystem productivity (Petchey et al. 2004) or stability (Valone and Schutzenhofer 2007). However, the index used in most of these studies is the number of functional groups defined a priori (for example for plants: grasses, legumes and herbs). This clustering may lead to a loss of information (Fonseca and Ganade 2001) or worst, may lead to a weak explanatory power on ecosystem processes (Wright et al. 2006). As an alternative, continuous indices of functional diversity, directly based on functional traits, have been proposed (see Petchey and Gaston (2006) for a review) but they are either highly correlated to species richness (Petchey and Gaston 2002) or designed for single trait approaches (Mason et al. 2005). To overcome these two limitations, Villéger et al. (2008a) recently generalized the framework of Mason et al. (2005) and proposed three indices to measure three independent facets of functional diversity (richness, evenness and divergence) designed for multi-traits case study. Splitting functional diversity into three independent components has already been relevant to elucidate processes of community assembly (e.g.

Mason et al. 2008). However, to our knowledge, there is no study that focuses on long-term modifications in the whole functional and multidimensional structure of communities when facing environmental changes. In the present study, we propose to investigate how the various facets of fish functional diversity were affected by abiotic shifts and habitat degradation in an estuarine ecosystem.

In addition to biodiversity measures, the degree of specialization is a complementary aspect of community structure (Julliard et al. 2006, Devictor et al. 2008). Indeed, when considering a regional pool of species, it is informative to determine whether the species of a local community are a random sample of the regional pool, or if they tend to exhibit more or less specialized trait combinations. Indeed, it has been hypothesized that specialist species are the most affected by environmental changes (e.g. for habitat specialists in Jiguet et al. 2007) since they are supposed to be strongly associated to particular niches. Thus if environmental changes lead to the degradation or even a loss of these niches, specialist species will be deeply affected. On the contrary, generalist species may tolerate a loss of particular habitats as they are supposed to occupy several ones and the most common. Hence, in addition to the modifications in the functional diversity of fish communities, we also investigated changes in their degree of functional specialization after abiotic shifts and habitat degradation.

Tropical estuarine ecosystems are distributed on several continents and are of primary interest both on ecological and socio-economical points of view (Constanza et al. 1997). Indeed, they are marked by a high biodiversity and they provide ecosystem services of high value (protein supply through fishing, water filtration, nursery habitats for juveniles) while they are severely impacted by mangrove deforestation, over fishing, aquaculture and urbanization (Lotze et al. 2006). They are also characterized by strong environmental variations through space and time due to mixed effects of freshwater inputs and marine influences. Large estuarine ecosystems yield a high diversity of habitats such as mangrove swamps, seagrasses beds, muddy or sandy sediments. These different habitats and their associated communities are not expected to respond in the same ways when facing disturbances. For instance, many studies have reported seagrass loss following drastic environmental changes induced by human influence such as eutrophication (Lotze et al. 2006, Orth et al. 2006). In turn, these modifications in the composition of these vegetated seabeds may alter their quality as habitat for associated fish and invertebrates with, as a consequence, a loss of some ecosystem functions and a decrease of the secondary productivity (Micheli et al.

2005). In these coastal ecosystems, the nekton is dominated by fish which play an important role in nutrient fluxes, both along the trophic level and through space with migrations (Holmlund and Hammer 1999). Investigating changes in the functional structure of fish communities will shed light on the influence of habitat degradation on two overlooked facets of community structure: functional diversity and functional specialization.

Terminos lagoon is one of the largest Mexican lagoons. It is of primary interest for biological conservation and fishery activities and it has been severely impacted by anthropogenic pressures during the last decades (shrimp fishery, urbanization of Carmen Island and deforestation of the watershed for intensive agriculture). Previous studies have underlined a strong shift in environmental conditions during the last two decades (Ramos Miranda et al. 2005a) as well as changes in the trophic structure of fish assemblages (Sosa Lopez et al. 2005). Our study aims to assess changes in the functional diversity of fish communities in the Terminos lagoon after a period of increasing disturbance and habitat degradation. These changes in functional diversity will be compared to changes in species richness and a new paradox in the response of communities to environmental pressure will emerge.

Material and methods

The study system

Terminos lagoon (Figure 1) is located in the south-western part of the Gulf of Mexico (Campeche State, Mexico). This is the largest lagoon in this area with a surface of 1660 km². Terminos lagoon is actually an estuarine ecosystem as it is strongly influenced by freshwater discharges from three streams located on its southern part (respectively from west to east: Palizada river, Chumpan river and Candelaria river).

The lagoon is delimited by the Carmen Island (30 km long and 2.5km wide) and thus water exchanges with the sea take place through two inlets, one on its north-eastern part (Puerto Real) and the other one on the north-western part (Carmen). The lagoon is very shallow with a mean depth of 3.5 m.

Water circulation in the lagoon generally follows a clockwise direction (David and Kjerfve 1998), with seawater going inside the lagoon through the Puerto Real inlet, mixing with freshwater near the stream mouths and the resulting brackish water goes outside the lagoon through the Carmen inlet (Figure 1).

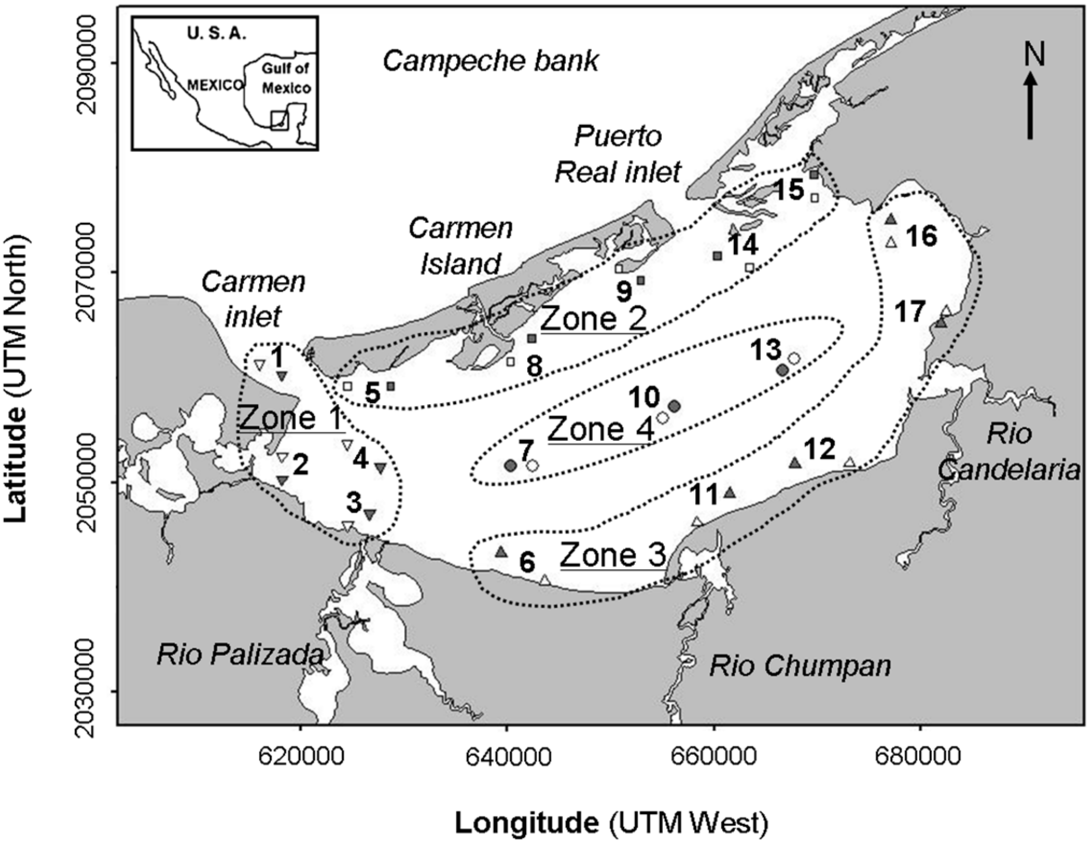

Figure 1 Map of the study area (Universal Transverse Mercator (UTM) coordinate system). White symbols represent the 17 sampling locations in 1980-81 whereas black ones are corresponding sampling locations in 1998-99. Environmental zones defined after environmental conditions recorded in 1980-81 are shapes with dotted black lines.

The climate is wet and tropical with three marked seasons, the dry season from February to May, the wet season from June to October and the “Nortes” or windy season from November to January with strong cold winds coming from the north.

Sampling protocol

Two similar biological surveys were conducted in 1980-81 (Yañez-Arancibia et al. 1982) and 1998-99 (Ramos Miranda, 2000). For each campaign 17 stations were sampled monthly during one year (Figure 1).

For each station and each month, fish communities were sampled using a shrimp-trawl (length: 5 m, mouth opening diameter: 2.5 m, mesh size: 19 mm) towed 12 minutes at a constant speed of 2.5 knots. The volume sampled was thus of 4,500 m^3. This active sampling method is well adapted to fishes living in this shallow coastal area since they are relatively small (< 30cm) and slow swimmers. For each sample, all individuals were identified at the species level and weighted to the nearest decigram.

Additionally, six environmental variables were recorded: depth, transparency (measured with a Secchi disk), temperature and salinity both at the top and the bottom of the water column. According to the monthly environmental conditions observed in 1980-81, the 17 stations were clustered into environmental zones (Ward agglomerative method on Euclidean distances after the standardization of environmental variables). In each zone, temporal changes between the two periods were tested for each environmental parameter using Wilcoxon pairwise rank tests since the same stations were sampled.

Functional characterization of fishes

Ecomorphological traits have been used for several decades to assess fish ecological niches and then to seek (*i*) interregional convergence (Winemiller 1991, Boyle and Horn 2006), (*ii*) assembly rules in fish communities (Bellwood et al. 2002, Mason et al. 2008) and (*iii*) relationships between fish traits and environments (Wainwright et al. 2002, Mouillot et al. 2007). These traits were assimilated to functional traits as they describe how key functions are performed by fishes. For instance, the ratio of gut length to standard length indicates fish trophic status (Kramer and Bryant 1995; Elliott and Bellwood 2003).

We evaluated functional diversity in fish communities for two key functions: food acquisition and locomotion. Since these functions of interest are complex processes, they cannot be described using only one trait (Dumay et al. 2004, Bellwood et al. 2006, Mason et al. 2007). For example, swimming ability combines several performances such as speed, endurance and manoeuvrability (Webb 1984) and thus cannot be summarized using one functional trait only. We thus selected respectively 7 and 10 ecomorphological traits to describe each function (Table 1). From these 16 traits, three are novel while five have been adapted from previously proposed traits.

Table 1 List of 16 functional traits, abbreviations, formula and relevance for each function of interest. For the two functions, the logarithm of body mass, log (Mass+1), was also considered as a functional trait. Description of morpho-anatomical measures and corresponding codes are presented in figure 1.

	Functional trait	**Code**	**Formula**	**Function**
Food acquisition	Oral gape surface	***Osf***	$\frac{Mw \times Md}{Bw \times Bd}$	Relative to maximum prey size or ability to water filtering (adapted from Karpouzi and Stergiou 2003)
	Oral gape shape	***Osh***	$\frac{Md}{Mw}$	Relative to prey shape and food acquisition (Karpouzi and Stergiou 2003)
	Oral gape position	***Ops***	$\frac{Mo}{Hd}$	Relative to position of preys in the water column (adapted from Sibbing and Nagelkerke 2001)
	Gill raker length	***GRlst***	$\frac{GRl}{Hd}$	Relative to filtration capacity or gill protection (adapted from Sibbing and Nagelkerke 2001)
	Gut length	***Glst***	$\frac{Gl}{Bl}$	Relative to digestibility of food (Kramer and Bryant 1995)
	Eye size	***Edst***	$\frac{Ed}{Hd}$	Relative to prey detection (adapted from Boyle and Horn 2006)
Locomotion	Eye position	***Eps***	$\frac{Eh}{Hd}$ *	Relative to position in the water column (Gatz 1979)
	Body transversal shape	***Bsh***	$\frac{Bd}{Bw}$	Relative to position in the water column and hydrodynamism (Sibbing and Nagelkerke 2001)
	Body transversal surface	***Bsf***	$\frac{\ln\left(\left(\frac{\pi}{4} \times Bw \times Bd\right)+1\right)}{\ln(Mass+1)}$	Relative to mass distribution along the body and hydrodynamism
	Pectoral fin position	***PFps***	$\frac{PFi}{PFb}$ ^{o}	Relative to maneuverability and position in the water column (Dumay et al. 2004)
	Aspect ratio of the pectoral fin	***PFar***	$\frac{PFl^2}{PFs}$ ^{o}	Relative to propulsion and/or maneuverability (adapted from Fulton et al. 2001)
	Caudal peduncle throttling	***CPt***	$\frac{CFd}{CPd}$	Relative to swimming endurance (Webb 1984)
	Aspect ratio of the caudal fin	***CFar***	$\frac{CFd}{CFs}$ #	Relative to endurance, acceleration and/or maneuverability (Webb 1984)
	Fins surface ratio	***Frt***	$\frac{2 \times PFs}{CFs}$ #	Relative to the swimming type (pectoral or caudal fin propulsion)
	Fins surface to body size ratio	***Fsf***	$\frac{(2 \times PFs)+CFs}{\frac{\pi}{4} \times Bw \times Bd}$	Relative to endurance, acceleration and/or maneuverability

* for flatfishes, $Eps = \frac{2 \times Ed}{Hd}$ as the two eyes are on the "top" of the head

^{O} flatfishes were considered without functionally pectoral fins, so *PFps* and *PFar* were fixed to 0

$^{\#}$ for species without caudal fin, *CFar* and *Frt* were fixed to 0

All these traits, except the logarithm-transformed mass (trait common to the two functions), are ratios of morpho-anatomical measures (17 morphological and 2 anatomical traits, Figure 2). For example, the aspect ratio of the caudal fin is obtained by dividing the square of its depth by its surface.

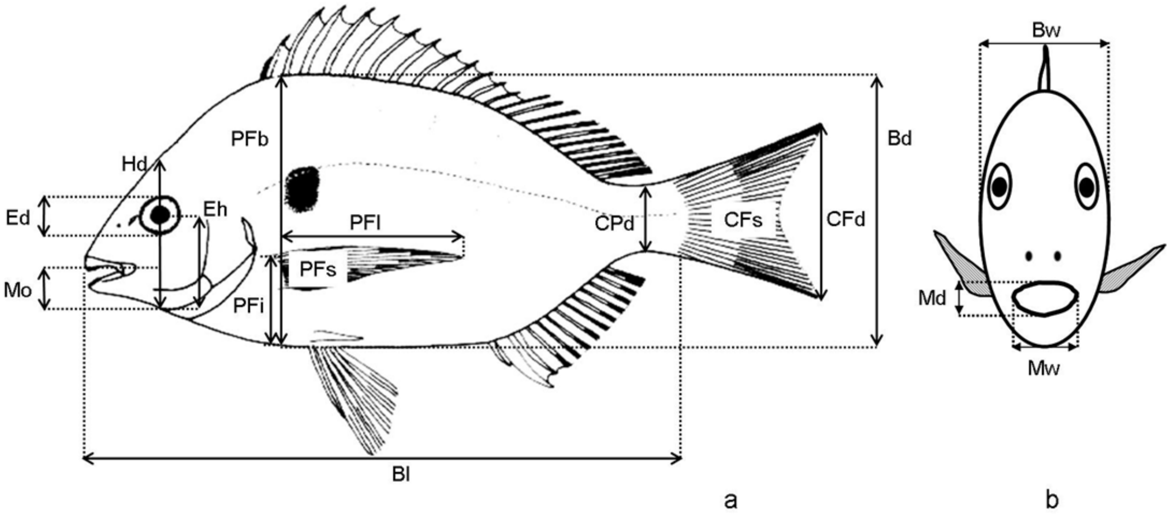

Figure 2 Morphological traits measured on digital pictures (a): *Bl* body standard length, *Bd* body depth, *CPd* caudal peduncle minimal depth, *CFd* caudal fin depth, *CFs* caudal fin surface, *PFi* distance between the insertion of the pectoral fin to the bottom of the body, *PFb* body depth at the level of the pectoral fin insertion, *PFl* pectoral fin length, *PFs* pectoral fin surface, *Hd* head depth along the vertical axis of the eye, *Ed* eye diameter, *Eh* distance between the centre of the eye to the bottom of the head, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis ; and with an electronic caliper (b) : *Bw* body width, *Md* mouth depth, *Mw* mouth width.
For flatfishes, body depth and width, mouth depth, width and position, and eye position were measured relatively to the position of the fish in its environment; in other words, the lateralization was not considered.

Individual biomass was measured with an electronic balance (precision 0.1g). Body width, mouth width and mouth depth were measured using an electronic caliper (precision of 0.1mm). The 14 other morphological traits were measured on digital pictures with a precision of 0.1 mm (camera: Canon Powershot G6, resolution: 7 millions of pixels) thanks to the software ImageJ. The length of the longest gill raker was estimated using a stereomicroscope (precision of 0.1mm). The gut (from the esophagus to the anus) was extracted by dissection, stretched and measured to the nearest millimeter.

Our set of traits is not designed for a restricted family or morphology, so it can potentially be used for all fish communities from fresh and marine waters. However, for particular morphologies (species without tail, flatfishes, rays), conventions were used for morphological measures (Fig. 2) and functional trait estimations (Table 1).

During a biological survey conducted in 2006-2007 in the same region (see Villéger et al. 2008b), a maximum of 20 individuals by species were randomly selected. On each of these individuals, morpho-anatomical traits measured and eco-morphological traits were calculated. For each species, the mean trait values were computed from individual measurements assuming that intraspecific variations were lower than interspecific variations (Dumay et al. 2004).

Measuring functional diversity

Measuring functional diversity has been achieved in many ways during the last two decades but progresses towards continuous and multivariate measures have been made.
Indeed, for a given community, functional diversity is nothing else than the distribution of species and of their abundances in a multidimensional functional space defined by traits (Figure 3). It thus appears difficult to embrace the whole definition of functional diversity – the diversity of functional traits - using only one index. Therefore, Villéger et al. (2008a), following the framework of Mason et al. (2005), proposed three complementary indices to evaluate the three primary and independent facets of functional diversity. Here we propose to use this multifaceted framework to evaluate modifications in the functional diversity of Terminos fish assemblages after environmental changes.

The first facet of functional diversity is functional richness which represents the amount of functional space filled by the community (Figure 3a). We propose to estimate functional richness by the volume inside the envelope that contains all trait combinations represented in the community, which basically corresponds to a multivariate functional range (*FRic* of Villéger et al. 2008a following Cornwell et al. 2006). More formally, this measure quantifies the volume inside the minimum convex hull containing all the species belonging to the community (see Annexe A for more details). Therefore, functional richness is only influenced by the identity of species (their abundances do not matter) and more particularly by the most extreme species (in terms of functional traits) which delimitate the convex hull. Therefore, functional richness is an incomplete description of functional diversity since it does not describe how the functional volume occupied is filled by the assemblage (Villéger et al. 2008a).

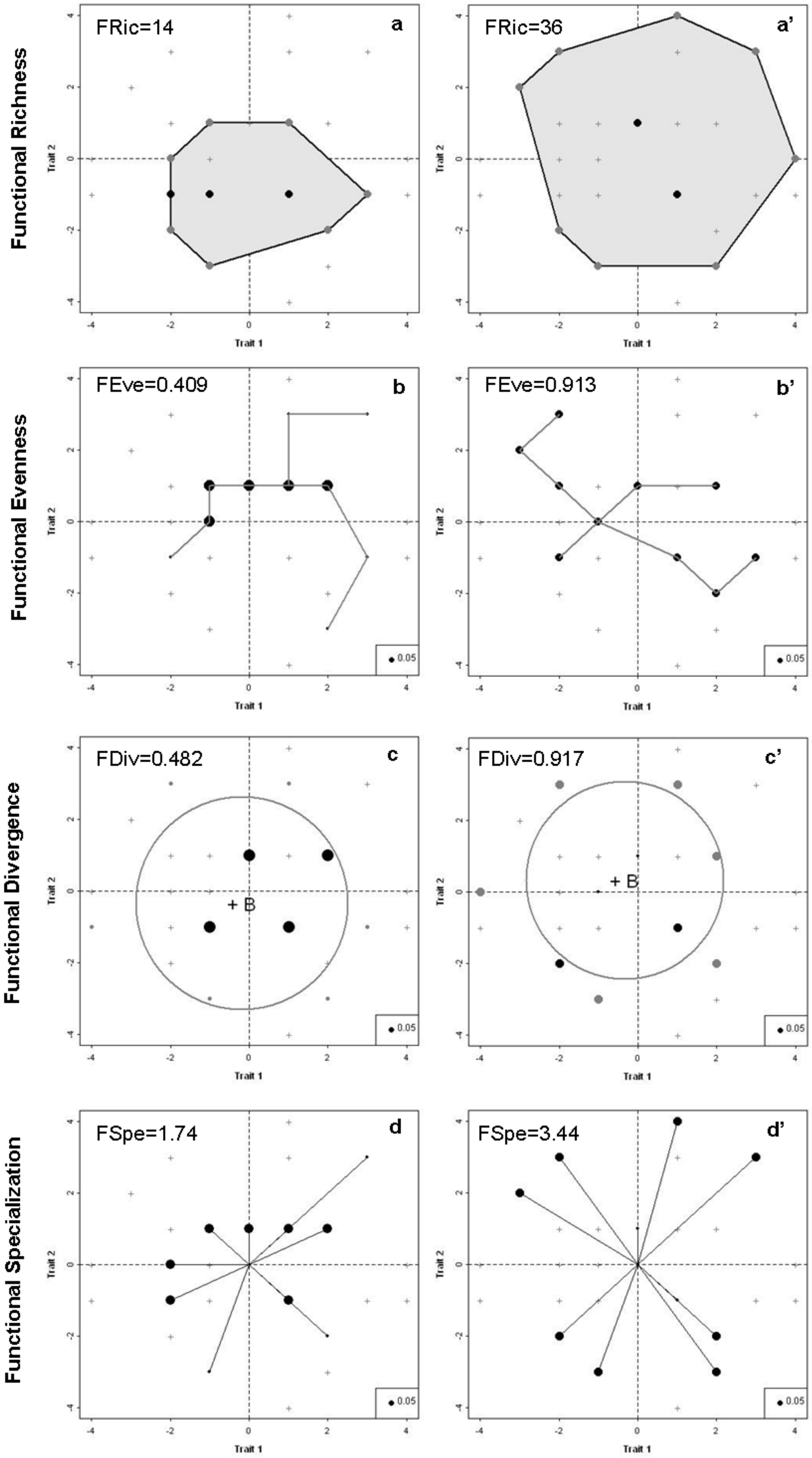
Functional Richness
FRic=14
a
FRic=36
a'
Functional Evenness
FEve=0.409
b
FEve=0.913
b'
Functional Divergence
FDiv=0.482
c
FDiv=0.917
c'
+ B
Functional Specialization
FSpe=1.74
d
FSpe=3.44
d'
0.05
Trait 1
Trait 2
-4
-2
0
2
4

Figure 3 Geometrical presentation of functional diversity indices and specialization. For commodity, only two traits are considered. Functional space is thus the two-dimensions geometrical space defined by the two traits. For the eight panels a local community of 10 species (represented by circle) is considered among a regional pool of 25 species (grey crosses). Species are plotted in this space according to their respective traits values while the disk areas are proportional to their abundances. Functional diversity of a community is thus the distribution of the species and of their abundances in this functional space. The three facets of diversity are decomposed in the a,b and c panels. First, functional richness (*FRic*) is basically the functional space occupied by the community (a). It could be estimated by the volume (here the area shaded in grey) inside the convex hull (black line).
Functional evenness (*FEve*) described the regularity of functional space occupancy (b). It could be estimated by the regularity of the distribution of the species and of their abundances on the minimum spanning tree (grey line joining all species).
Functional divergence (*FDiv*) estimates the divergence of biomass inside the functional volume occupied by the community (c). It could be estimated by the abundance-weighted deviation to the mean distance (black circle) to the centre of gravity of the points shaping the convex hull (named B, plotted by a black cross).
Functional specialization is a complementary aspect of community structure (d). For commodity, traits have been standardized so that mean is 0. Thus centre of gravity of the 25 species is the point of coordinates (0,0). Specialization of a species is then the Euclidean distance to this point (black lines). Specialization of a local community (*FSpe*) is finally the abundance-weighted mean of the specialization of the species belonging to the community.
For each facet of functional diversity and for functional specialization, an increase of the index is illustrated on the right column (respectively a’, b’, c’, d’).

Functional evenness – defined as the evenness of abundance distribution in a multidimensional functional space - was the second facet proposed to complement functional richness (Mouillot et al. 2005). Villéger et al. (2008a) proposed an index, named *FEve*, derived from the *FRO* introduced by Mouillot et al. (2005) to quantify the regularity with which species abundances fill the functional space (Figure 3b). Basically the measure proposed by Villéger et al. (2008a) includes both the regularity of species distribution and the regularity of their abundances along the “skeleton” (represented by the Minimum Spanning Tree) of the functional volume occupied. This index is constrained between 0 and 1, and decreases either when functional distances among species are less even or when abundances are less evenly distributed among species, i.e. when the main abundances belong to functionally close species. However, functional evenness does not tell anything about the distribution of species abundances from the centre to the edge of the functional space while the abundance of species with extreme traits compared to those with common traits is also important in functional ecology (e.g. Bellwood et al. 2004).

As a response, a third facet of functional diversity, functional divergence, was introduced to quantify whether higher abundances are close to the edge of the volume occupied by species (Figure 3c). The index proposed by Villéger et al. (2008a), named *FDiv*, ranges between 0 and 1 (see Annexe A for formula). The index approaches zero when highly abundant species are very close to the centre of gravity of the volume occupied and it approaches unity when highly abundant species are very distant from the centre of gravity.

FEve and *FDiv* indices take into account species abundances but are unitless since they use relative abundances. Moreover, these three indices are a priori independent of each other and thus are not trivially linked (Villéger et al. 2008a). The only restriction to the use of these three indices in combination is that the number of species must be strictly higher than two and than the number of traits.

Specialization of communities

Specialization of a community is basically the average specialization of its species. An index to measure specialization of a species within the context of functional traits was proposed by Bellwood et al. (2006). When species are plotted in a functional space according to their trait values, the degree of specialization for a species is the Euclidean distance of this species to the centre of gravity of all the species contained in the regional pool (Figure 3d). Thus a species is more specialized as it is more distant in terms of functional traits from the mean of the global species pool.

Mathematically, considering N species in a regional pool, the coordinates of the centre of gravity G $(g_1, g_2, ..., g_T)$ of these N species are calculated as:

$g_k = \frac{1}{N}\sum_{j=1}^{N} x_{jk}$, where x_{jk} is the coordinate of species j on trait k [1, T].

Now, consider a species j for which coordinates on the T axes (i.e traits values) are $(x_{j1}, x_{j2}, ..., x_{jT})$. Its Euclidean distance to the centre of gravity dG_j, is thus: $dG_j = \sqrt{\sum_{k=1}^{T}\left(x_{jk} - g_k\right)^2}$.

Therefore, for a local community i with S species ($S \leq N$) having specialization values of $(dG_1, dG_2, ..., dG_S)$ and relative abundances $(w_1, w_2, ..., w_S)$, the functional specialization index of this community $FSpe_i$, is : $FSpe_i = \sum_{j=1}^{S}\left(w_j \times dG_j\right)$.

From a geometrical point of view the functional specialization of a community depends of species positions relatively to the centre of gravity calculated from the regional pool while functional diversity indices depend only on the functional structure of the target community. These two aspects are thus two complementary views of the functional structure of species communities.

Assessing changes in the functional structure of fish communities

For each function, trait values of all the species present in the lagoon were standardized so that mean of each trait was 0 and its standard deviation was 1. This standardization aims to give the same weight to each trait in the estimation of functional diversity. Consequently, in our case, the degree of specialization corresponds to the distance of species to the origin of the functional space which coordinates are (0, 0, …, 0).

We estimated species abundances thanks to biomass rather than number of individuals because biomass, through metabolism, is more related to functional effects of species in ecosystems (Grime 1998). Let consider a zone (Figure 1) where Z communities (12 months x number of stations) were sampled with a species richness of S for this strata. For each community i, we knew the biomass b_{ij} of species j. We then computed the relative biomass f_{ij} of species j in community i using: $f_{ij} = \dfrac{b_{ij}}{\sum_{j=1}^{S} b_{ij}}$.

Similarly, the relative weight of each community i in the target zone was estimated using

$$p_i = \frac{\sum_{j=1}^{S} b_{ij}}{\sum_{i=1}^{Z}\sum_{j=1}^{S} b_{ij}}.$$

Finally, the relative abundance r_j of species j in the zone could be deduced:

$$r_j = \frac{\sum_{i=1}^{Z} b_{ij}}{\sum_{i=1}^{Z}\sum_{j=1}^{S} b_{ij}} = \sum_{i=1}^{Z}\left(f_{ij} \times p_i\right).$$

For each function, the three functional diversity indices and the specialization index were computed in each zone for each period, based on trait values and relative biomasses of species

(Figure 4). Then for each function and for each zone the differences values between 1998-99 and 1980-81 were calculated for the four indices (specialization and functional diversity).

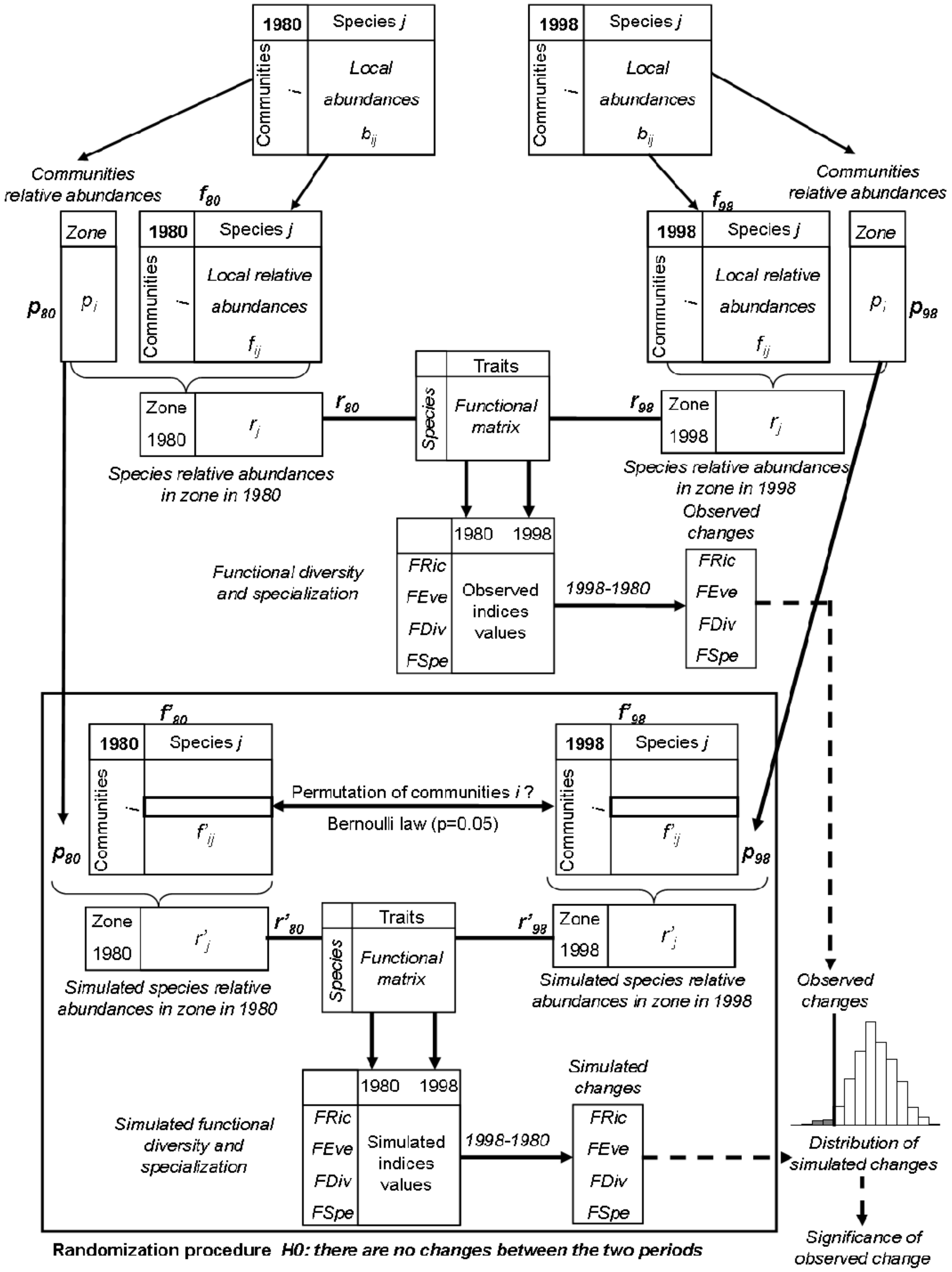

Figure 4 Summary of data analysis and randomization procedure

These changes in index values cannot be interpreted directly since fish communities have different species numbers and different biomasses between the two periods. Thus the question is no longer whether observed functional diversity indices are lower in 1998-99 than in 1980-81 but whether functional diversity indices are significantly lower in 1998-99 than in 1980-81 after randomizing the samples between the two periods. We thus tested the null hypothesis positing that there was no change in the functional structure of fish communities between the two periods. Thus we designed an appropriate randomization procedure to test temporal changes in functional diversity indices for each function and each zone (Figure 4).

Since a randomisation procedure to test a null hypothesis has to keep every feature of the observed data, except the feature that the study aims to test we did not modify the spatio-temporal structure of the sampling design nor the observed relative abundances in fish communities. For each zone, there are Z communities sampled for each period. There are thus two matrices (Z x S), noted f_{80} and f_{98}, containing relative biomasses of species j in station i (f_{ij}). Similarly, there are two vectors, noted p_{80} and p_{98}, containing the Z values of relative weight of each community (p_i). For each pair of communities (i.e same station sampled the same month for the two periods), a Bernoulli law (mean of 0.5) was used to decide if the corresponding lines in f_{80} and f_{98} have to be permuted. At the end of this random process, we obtained two new matrices of relative abundances in the communities (f_{ij}), named hereafter f_{80}' and f_{98}'. Relative biomasses of species j at the zone level (r_{j80}' and r_{j98}') were computed using:

$$r_{j80}' = \sum_{i=1}^{Z}\left(f_{ij_{80}}' \times p_{i80}\right) \text{ and } r_{j98}' = \sum_{i=1}^{Z}\left(f_{ij_{98}}' \times p_{i98}\right).$$

Functional diversity indices and the specialization index were then calculated considering trait values and relative biomasses obtained randomly (r_{j80}' and r_{j98}'), and finally the corresponding differences between the two periods were calculated.

Basically, this null model randomized the year to which each sample belongs but without modifying abundance patterns between samples and spatio-temporal structure of the sampling design. Hence, this procedure takes into account any autocorrelation (temporally or spatially) among the samples.

This process was carried out 9999 times for each function and each zone. The risk to reject the null hypothesis while it is valid associated to this null model is the proportion of simulated values inferior or superior to the observed one (p) (Manly 1998). Thus, considering a bilateral test with a total risk of 5%, when $p<0.025$ then observed change between 1980 and

1998 is lower than expected under the null hypothesis whereas when $p>0.975$ observed change is higher than expected.

The clustering of stations, the computations of indices, randomizations for the null model and statistical analyses were carried out using R software (R development core team 2008). Scripts used to compute functional diversity and functional specialization indices are available online (http://www.ecolag.univ-montp2.fr/software).

Results

Data collection

A total of 10 449 and 11 946 individuals were respectively caught in 1980-81 and 1998-99 for respective weights of 423 and 281 kg. A total of 103 species were caught with respectively 77 species in the 80's and 89 in the 90's. Actually, 14 species disappeared while 26 appeared after 18 years in the catches, revealing a global increase of species richness and a strong species turnover at the lagoon scale.

The 19 morpho-anatomical measures were estimated on 948 individuals belonging to 62 species. Among these 62 species, the 16 functional traits were estimated on 20 individuals for 38 species and on more than 10 individuals for 47 species. Overall species for which traits have been measured represent 98.77% of total biomass for the two periods.

Spatial stratification

Clustering of the 17 stations according to their environmental conditions in 1980-81 led to the discrimination of 4 zones (Figure 1, Table 2). These zones are geographically continuous and reflect hydrology and sedimentology. Zone 1 grouped the stations near the Carmen Inlet and is marked by the influence of stream discharges (particularly from Palizada River, which has the highest debit with more than $4x10^9$ m^3 by year), and thus a large amplitude for salinity (from 4 to 35 psu). Substrate in zone 1 is muddy with fine sand and clayed silt. Zone 2 stretched along Carmen Island up to Puerto Real inlet where stations are under marine influence (mean salinity of 28.5 psu). Substrate varies from muddy areas near mangrove swamps (*Rhizophora mangle*) to sandy zones colonized by seagrasses (*Thalassia testudinum*). Zone 3 is along the southern coast of the lagoon. These shallow waters (mean depth of 2.5m) close to mangroves received influences of Candelaria and Chumpan rivers and have silt-clay sediments. Zone 4 is in the centre part of the lagoon, which is the deepest (mean depth of 3.9m) and is a transitional zone between marine and freshwater influences (salinity ranges from 15 to 36 psu for a mean of 26 psu).

Table 2 Environmental conditions in the four zones. For each zone the first line contains the mean value for 1980-81. Data in italics are corresponding values in 1998-99. Spatio-temporal coefficients of variation are in parenthesis. Results of pair wise Wilcoxon rank test between the two periods are given under the second value: ^{NS} non significant, * p<0.05, ** p<0.01, *** p<0.001.

Zone	Year	Depth (m)	Secchi (m)	Bottom salinity (psu)	Substrate
Zone 1	1980-81	2.8 (22%)	0.6 (35%)	21.3 (41%)	Muddy with fine sand and clayed silt, riverine influence.
	1998-99	*2.1 (45%)*	*0.5 (50%)*	*23.1 (47%)*	
	difference	***	*	NS	
Zone 2	1980-81	2.6 (32%)	1.1 (45%)	28.5 (25%)	Mud near mangrove swamps and sand with seagrasses and macroalgae.
	1998-99	1.6 (45%)	0.9 (49%)	31.7 (18%)	
	difference	***	**	***	
Zone 3	1980-81	2.5 (24%)	0.9 (38%)	22.4 (28%)	Silt-clay sediments, mangrove swamps, riverine influences
	1998-99	*1.3 (35%)*	*0.6 (39%)*	*25.9 (22%)*	
	difference	***	***	***	
Zone 4	1980-81	3.9 (11%)	1.1 (36%)	26 (25%)	Sand-silt sediments
	1998-99	*3.9 (9%)*	*1.3 (44%)*	*31.1 (17%)*	
	difference	NS	NS	***	

Environmental changes

Comparisons between the two periods showed that the four zones experienced severe modifications in their environmental conditions (Table 2). Depth was globally decreasing particularly in zones 1, 2 and 3. For instance depth in zone 2 significantly dropped from 2.6m on average in 1980 to 1.6m in 1998 (Wilcoxon pair wise rank test: $p<0.001$). Similarly transparency significantly decreased in these three zones (in zone 2 from 1.1 to 0.9m, $p<0.01$). Salinity was higher in 1998-99 than in the 80's particularly in zones 2, 3 and 4 which all showed a significant increase (more than 3psu on average, $p<0.001$).

Changes in fish richness and fish biomass

Species richness in the zones increased from 30 to 76 between the two periods, with zone 4 being the poorest zone while zone 2 is the richest (Table 3). As explained before, species richness increased between 1980 and 1998 and this global trend was particularly due to zone 2 where species richness increased from 56 to 76 fish species. On the contrary species richness dropped from 57 to 50 in zone 3.

Zone 2 had the highest biomass for the two periods (respectively more than 60 and 40% of total biomass) but exhibited a strong decrease from 258 to 120kg after 18 years.

Table 3 Ecological changes in each zone between the two periods of study (1980-81 and 1998-99). For each cell, the value in 1980-81 is on the left whereas the value in 1998-99 in on the right. Differences in communities' structure between the two periods were assessed using the Bray-Curtis index. The two last columns present respectively the number and the contribution to the total biomass of the species on which functional traits have been measured.

		Year	Zone 1	Zone 2	Zone 3	Zone 4
Species richness		1980-81	49	56	57	30
		1998-99	48	76	50	36
Total biomass (kg)		1980-81	57	258	82	21
		1998-99	54	120	87	15
Bray-Curtis dissimilarity			0.41	0.66	0.47	0.57
Species functionally described	Number	1980-81	42	42	45	25
		1998-99	43	49	44	31
	% of biomass	1980-81	98.64	98.95	99.12	99.63
		1998-99	99.80	97.3	99.48	97.51

Bray Curtis dissimilarity index was calculated between the two periods for each zone. Values were relatively high, ranging from 0.41 to 0.66 (mean 0.53) revealing that fish community structures (species identity and their abundances) have been strongly modified between the two periods.

Changes in functional diversity and functional specialization

One step further we analysed changes in term of functional diversity and functional specialization. Results of null models, testing for the period effect, provided contrasted conclusions between zones (Table 4). For instance, the centre part of the lagoon (zone 4), presented no significant modification in functional structure of fish communities neither in terms of diversity nor in terms of specialization for both food acquisition and locomotion. When compared to the strong modification in community composition (Bray-Curtis dissimilarity index of 0.57), it means that even if species turnover was strong it had no influence on the functional structure of fish communities.

Table 4

Changes in functional diversity facets and in functional specialization in each zone between the two periods of study (1980-81 and 1998-99). For each function, each zone and each index, observed differences between the two periods were tested again a null-model positing that there was no change between the two periods.

“-“ indicates a change significantly lower than expected

“+“ indicates a change significantly higher than expected

Results on the left of the cell are for food acquisition whereas results for locomotion are on the right.

	Function	Zone 1	Zone 2	Zone 3	Zone 4
Functional richness	Food acquisition	-			
	Locomotion				
Functional evenness	Food acquisition		+		
	Locomotion				
Functional divergence	Food acquisition	+	-		
	Locomotion		-		
Functional specialization	Food acquisition		-	+	
	Locomotion	-	-		

At the opposite, the northern part near Carmen Island (zone 2) was the most affected zone. Indeed, for both food acquisition and locomotion, functional divergence and functional specialization were significantly lower in 1998 than in 1980 (Figure 5). In this zone, drastic changes in term of dominance occurred among the main species (i.e. those for which relative biomass is higher than 5%). For example, the most abundant species in 1980 was the Western Atlantic seabream *Archosargus rhomboidalis* (Sparidae) while the most abundant became the striped mojarra *Eugerres plumieri* (Gerridae) in 1998. This latter species accounted for more than 20% of the total biomass in 1998 whereas only 2 individuals were caught in 1980. Another gerid, the caitipa mojarra *Diapterus rhombeus*, showed the same pattern, becoming the third ranked species in 1998 with more than 11% of the total biomass. On the contrary, the checkered puffer (*Sphoeroides testudineus*, Tetraondontidae) dropped from 26% of total biomass to only 7.5% in 1998. The third “loser” species is the hardhead sea catfish *Ariopsis felis* which almost disappeared whereas it represented more than 14% of fish biomass in 1980. On the contrary, a very functionally similar species to *Ariopsis felis*, the dark sea catfish *Cathorops melanopus*, has slightly increased (from 6 to 9% of total biomass).

These strong dominance modifications observed in zone 2 provoked changes in the functional structure of fish communities in terms of functional diversity and of functional specialization (illustrated for food acquisition on Figure 4). Indeed, as the checkered puffer and the Western Atlantic seabream are specialists for food acquisition (very distant for the center of gravity), their decrease in relative abundance coupled to the increase of the two mojarras, which are generalist species, led to a significant decrease for both divergence and specialization.

Few significant changes were observed in zones 1 and 3 assuming a low modification in the functional structure of fish communities despite a high species turnover. Functional richness of food acquisition decrease significantly in zone 1 while locomotion specialization also significantly decreased. In zone 3 we observed a significant increase in the specialization for food acquisition.

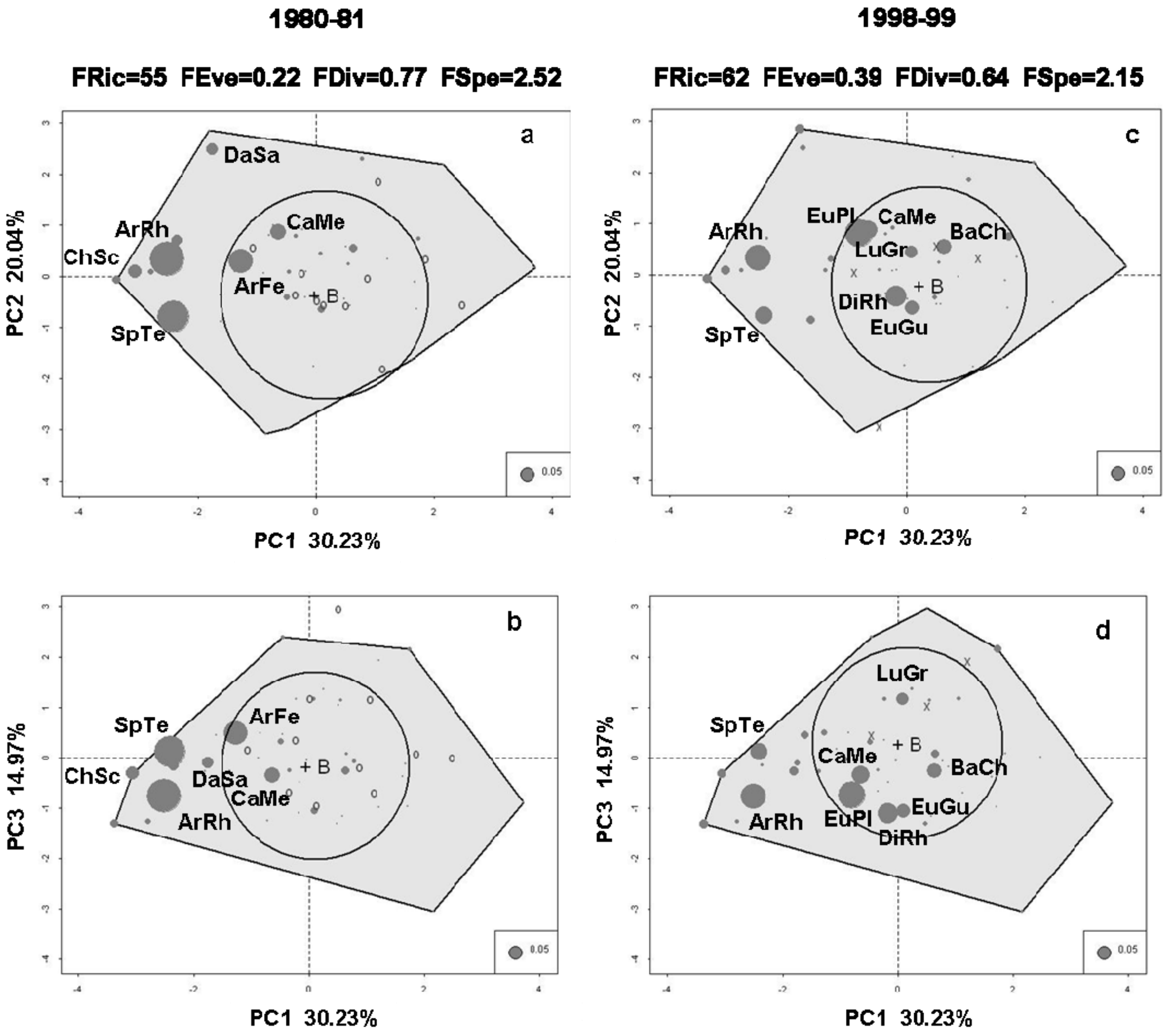

Figure 5 Changes in functional diversity and functional specialization for food acquisition in zone 2 between 1980 (a and b) and 1998 (c and d). The two first PCA plan are considered for convenience (respectively panels a and c for principal component 1 and 2 and b and d for 1 and 3). They explain more than 65% of the total variability. Graphical conventions are the same than in figure 2. Names of dominant species are coded as following: ArFe *Ariopsis felis*, ArRh *Archosargus rhomboidalis*, BaCh *Bairdiella chrysoura*, CaMe *Cathorops melanopus*, ChSc *Chilomycterus schoepfi*, DaSa *Dasyatis sabina*, DiRh *Diapterus rhombeus*, EuGu *Eucinostomus gula*, EuPl *Eugerres plumieri*, LuGr *Lutjanus griseus*, SpTe *Sphoeroides testudineus*. Grey “0” in panels a and b represent species absent in 1980 and present in 1998.Grey “X” in panel c and d represent species present in 1980 and not in 1998. Values of indices are given at the bottom of each period.

Discussion

While most previous works dealing with environmental influences on biodiversity have focused on species richness or community composition, we proposed here to go further and to assess changes in the functional structure of fish communities following environmental shifts and habitat degradation. We used a large dataset resulting from a long term ecological survey in an ecosystem of major interest, both ecologically and economically. Terminos lagoon has been severely impacted between 1980 and 1998. First, environmental conditions showed a marinisation of waters as well as a global decrease of depth. These trends are particularly severe for zones 2 and 3 which lost more than one meter of depth after 18 years. Moreover, the mean salinity increase was associated to a decrease of variation in salinity through space and time (Table 2). In other words, there was a salinity homogenization across stations and months in each zone. Changes in fish communities are also marked with a global increase of more than 15% in species richness while one fourth of species present in 1980 has been replaced. Besides, standing biomass dropped severely, both at zone and lagoon scales. Overall, community compositions have also been deeply modified between the two periods, as illustrated by high values of Bray-Curtis dissimilarity indices in the four zones (Table 3). Ramos Miranda et al. (2005) already observed a significant decrease of taxonomic diversity despite the increase of species richness. This finding was due to the fact that new species occurring in the lagoon in 1998 belong to family or genus present before in the lagoon, whereas at the opposite species disappearing were not replaced by species of the same taxa. Facing to these contrasted biotic changes, it is a critical issue to go further by considering fish communities with a functional perspective.

In the northern part of the lagoon (zone 2), there is not only a strong increase in species richness (20 species more in 1998 than in 1980) but also a two fold decrease of biomass and drastic changes in term of species dominance. These modifications in community composition and structure induced changes in fish functional diversity. Two particular species partially replaced previously dominant ones and then deeply modified the functional structure of fish communities. The two “loser” species (the checkered puffer *Sphoeroides testudineus* and the Western Atlantic seabream *Archosargus rhomboidalis*) are functionally close for food acquisition as illustrated by their relative proximity on the PCA projection (Figure 5). Indeed, they are characterized by similar mouth size, shape and position and a long gut adapted to a diet mainly composed of small shellfishes and epiphytic algae. This highlights the interest of a functional approach to community structure as these species are taxonomically very different while functionally close (Figure 6). On the contrary, the two “winner” species are both gereids and have similar morphology except that *Eugerres plumieri* is bigger than *Diapterus rhombeus*. They are characterized by a small median mouth ended with a long protrusion, which is a typical adaptation for invertebrates capture in the water column. Moreover, the two loser species are generally associated to seagrass beds where they find benthic molluscs and plant material (McEachran and Fechhelm, 2005). On the contrary the two winner species do not have such dependence and are often associated to bare muddy areas (McEachran and Fechhelm, 2005). These results suggest that species turnover was non-random but, instead, was determined by habitat-trait relationships.

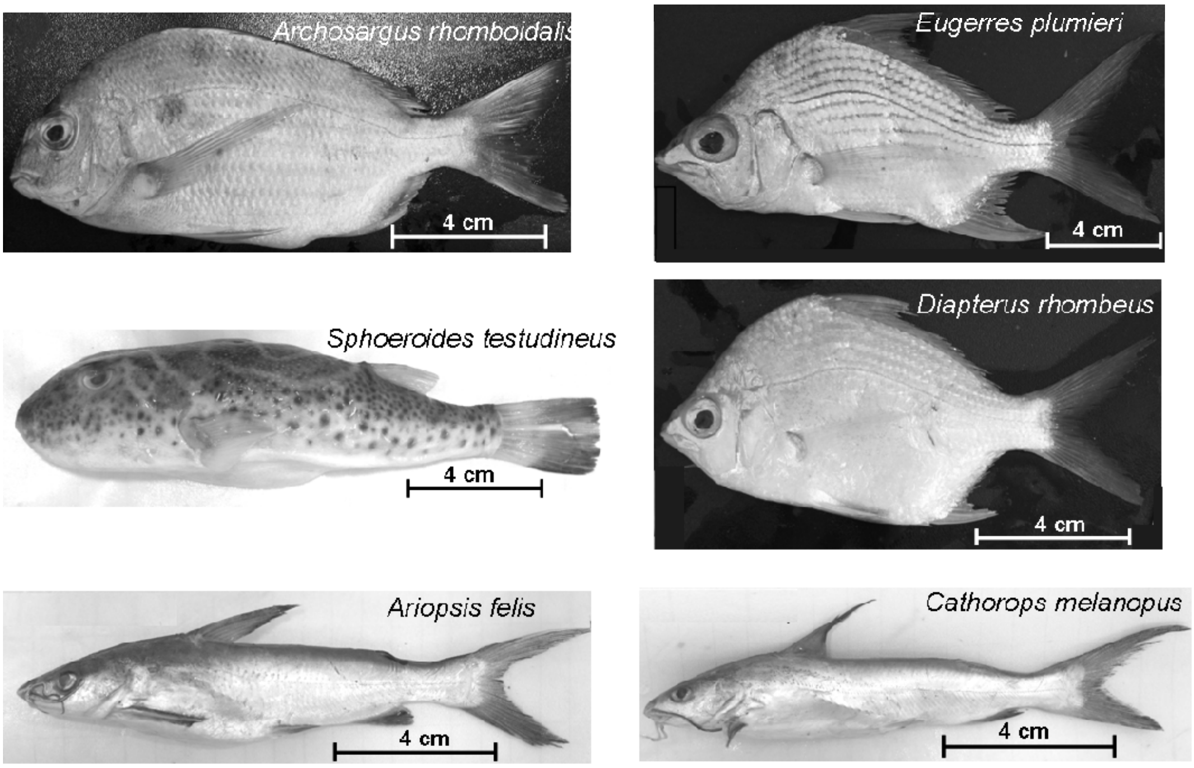

Figure 6 Pictures of the six dominant species in the northern part of Terminos lagoon. Species on the left were dominant in 1980-81 whereas species on the right were dominant in 1998-99

In the 80’s the shallow waters along Carmen Island were mainly covered by seagrass (data from 1981 in Yañez-Arancibia and Day 1988). During the nineties, seagrass coverage decreased all over this zone (Ramos Miranda and Flores Hernandez, personal observations), especially near the city of Carmen (station 5, figure1). This disappearance of *Thallasia* *testudinum* in this part of the lagoon could be related to the increasing turbidity which is among the major causes of seagrass meadows loss (Orth et al. 2006). These factors of stress may follow the destruction of some adjacent mangrove patches (Mas public communication, Ramos Miranda and Flores Hernandez, unpublished manuscript) and of the quick urbanization (the city of Carmen grew up from less than 50 000 inhabitants in 1980 to more than 150 000 in 2000). Indeed, mangroves often play an important ecological role by filtering nutrients and pollutants and preventing from excessive turbidity (Constanza et al. 1997). On the contrary, the urbanization in this area may have increase pollution and eutrophication due to waste waters. Finally, the decrease of this very particular habitat and of its associated benthic fauna and epiphytic vegetation may be the main driver of the strong decrease of associated species. It suggests that the replacement of seagrass patches by shallower muddy area have benefited to gerid species which share adapted traits. These results suggest that, in our system, trait-based mechanisms (opposed to trait-neutral) influence species turn-over and explain functional diversity loss (Suding et al. 2005).

Indeed, even if sea catfishes are classically associated to muddy substrate, *Ariopsis felis* adults are known to use shallow waters with seagrass as reproduction and nursery habitats (Yañez-Arancibia and Lara-Dominguez 1998). In our study, the abundance of *Ariopsis felis* is strongly decreasing not only in the inner part of Carmen Island (zone 2) but also in the other parts (for example it dropped from 15% of total biomass to less than 5% in the central part of the lagoon: zone 4). Moreover, the mean individual biomass of *A. felis* in this zone decreased strongly from 71 to 19g between the two periods, indicating a shift of occupation between mature adults and sub-adults. Thus, the degradation of a key habitat for reproduction could affect the entire population of *Ariopsis felis*. Conversely, *Cathorops melanopus* is described as a typical estuarine species that spent all its life-cycle inside the lagoon (Yañez-Arancibia and Lara-Dominguez 1998). Juveniles feed (mainly on organic matter and crustaceans) in zones influenced by river discharges before migrating at the sub adult stage to shallower waters near Carmen Island. Finally, adults breed in deep waters close to the centre of the lagoon. Between the two periods, relative abundance of *Cathorops melanopus* have increased in the entire lagoon, especially in the zone near stream mouth (zone 1) as it represents half of the biomass in 1998-99 (only 30% in 1980-81). These observations suggest that the shift in environmental conditions and the increasing influence of streams (particularly marked for stations 2 and 3) may have favoured this estuarine species to the detriment of *Ariopsis felis*.

The other parts of the lagoon seem to be functionally less affected by environmental changes which are nevertheless significant. However, communities' composition and structure have been deeply modified between the two periods in terms of species abundance turnover. Additionally, these zones are strongly affected by environmental seasonal variations, due to their exposition to freshwater discharges and/or marine influences. All these facts suggest that long term environmental changes do not have deeply changed theses muddy to sandy bare habitats. Therefore, species replacements occur between functionally redundant species and do not lead to changes in the functional structure of communities.

The contrasted results obtained on the four zones suggest that the lagoon had not responded in the manner between the two periods of study. The zone near the Carmen Island has been the most affected with strong changes in its functional structure for the two functions. Moreover these changes were not adequately reflected when considering only species richness or taxonomic composition and this clearly underlines the need to consider functional diversity and functional specialization in long term surveys. Our results are in accordance with the few studies dealing with the functional aspect of community changes when facing disturbance. Indeed Ernst et al. (2006) demonstrated that beyond a loss of species richness after selective logging there was a dramatic loss of functional diversity anuran communities. Devictor et al. (2008) found that more specialized species responded more negatively to landscape fragmentation and disturbance than generalist species. Here, one step further we show that different measures of biodiversity may lead to a paradox in the response to disturbance: a loss of functional diversity resulting from a loss a functional specialisation while species richness increases. This result highlights that species richness may provide a wrong signal of ecosystem recovery and that a multifaceted framework (including functional traits) in the assessment of biodiversity changes after disturbance is necessary. This result suggests that conservation effort should take into account the preservation of the diversity of functional traits in addition to the preservation of species richness in order to sustain ecosystem processes. To this aim, critical habitats such as seagrass beds need full attention. More generally the use of several diversity facets seems essential to detect the real dimension of biodiversity loss after anthropogenic disturbance. Towards this objective, the estimation of three complementary functional diversity indices in combination to the functional specialization index provides a complete framework to assess changes in the functional structure of communities under threat.

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Chapitre 7

Synthèse et perspectives

> Par quoi, tous les Hommes de bon esprit doivent mettre tout, leurs études, leur peine, leur industrie, en ce qu'ils puissent connaître les espèces et diversités, les causes, vertus et effets de toutes choses qui sont en la terre, en l'eau, en l'air.
>
> Guillaume Rondelet, *L'Histoire entière des poissons,* 1558

7.1 Des traits à la diversité fonctionnelle des communautés

7.1.1 Les traits fonctionnels chez les poissons : Vivement un consensus !!

Les résultats écologiques présents dans la littérature et ceux illustrés dans cette thèse (Manuscrits F et H) démontrent la pertinence de l'approche fonctionnelle des communautés de poissons, et la nécessité de prendre en compte les caractéristiques biologiques des espèces plutôt que leur simple identité taxinomique.

Toutefois, il est clair que l'écologie fonctionnelle des poissons est en retard par rapport aux nombreux travaux réalisés sur les plantes. Ceci peut s'expliquer par la plus grande complexité des fonctions assurées par les organismes animaux et par la plus grande difficulté à les décrire efficacement.

Historiquement, l'approche fonctionnelle des poissons remonte aux travaux en écomorphologie (Gatz 1979, Winemiller 1991). Cette vision ne fait pas directement référence à la définition évolutive des traits fonctionnels. Cependant, elle est directement reliée au concept de niche écologique, à la fois via le régime alimentaire (traits liés à l'acquisition de la nourriture) mais aussi via l'habitat (traits liés à la nage).

Contrairement à l'approche écomorphologique, l'approche « flux » s'intéresse uniquement aux capacités de biodégradation des poissons sans saisir la niche écologique de ces derniers. Néanmoins, cette approche plus « classique », permet de lier directement la composition des communautés aux processus écosystémiques (Flecker *et al.* 2002, McIntyre *et al.* 2008). Cette dichotomie dans l'approche fonctionnelle des poissons illustre la nécessité d'une unification de la discipline à travers un cadre d'étude commun. Pour cela, il est nécessaire de proposer une liste de fonctions d'intérêt écologique et les traits fonctionnels permettant de les quantifier.

Nous avons ainsi encouragé une vision intégrative de l'écologie fonctionnelle des poissons, en proposant un nombre restreint de traits pour chacune des fonctions biologiques majeures (Manuscrit A). Cette liste n'a pas vocation à être exhaustive ou optimale, mais nous espérons qu'elle suscitera une réflexion commune dans la communauté scientifique. Nous espérons en effet qu'un consensus émerge rapidement sur une liste de traits pertinents pour capturer la niche fonctionnelle des espèces de poissons. Il sera alors possible de mener des comparaisons inter-sites et des méta-analyses sur de larges bases de données.

A l'aide de ces données, il sera en particulier intéressant de mettre en évidence d'éventuelles convergences évolutives entre des assemblages d'espèces phylogénétiquement éloignées. De telles convergences suggèrent que l'environnement est un filtre puissant dans l'assemblage des espèces.

Une autre question clé à tester est la variabilité du niveau de redondance fonctionnelle entre les différents écosystèmes. Ainsi, la comparaison entre la richesse spécifique et la richesse fonctionnelle, permet de voir si les « hot spots » de diversité taxinomique sont aussi des « hot spots » de diversité fonctionnelle. Si oui, cela suggère que la quantité de niches disponibles influence la richesse spécifique et par cascade la richesse fonctionnelle. A l'inverse, si la redondance n'est pas corrélée à la richesse spécifique, alors en termes de conservation il est primordial de s'intéresser aux écosystèmes pauvres en espèces car ils sont plus sensibles à la perte d'une espèce.

D'un point de vue pratique, un formidable outil est déjà à disposition de la communauté ichtyologique avec le site internet *FishBase.org* (Froese & Pauly 2008) et il pourrait tout à fait servir de support au stockage de telles données.

7.1.2 Complémentarité théorique et pratique des indices de diversité fonctionnelle

La diversité fonctionnelle est un concept général décrivant la diversité des fonctions assurées par une communauté. En pratique, les fonctions sont décrites à l'aide de traits fonctionnels. Par analogie avec la notion de niche écologique (Hutchinson 1957), la diversité fonctionnelle peut alors être formalisée comme la répartition des espèces et de leurs abondances dans l'espace multidimensionnel défini par les traits fonctionnels (Rosenfeld 2002).

En se focalisant sur cette vision générale, nous avons ainsi proposé un nouveau jeu d'indices complémentaires (Manuscrit B) permettant de décrire les trois facettes de la diversité fonctionnelle (richesse, régularité, divergence). Outre ces indices, nous avons aussi esquissé un cadre d'application général pour relier la diversité fonctionnelle à l'environnement et aux propriétés écosystémiques.

Parmi, les nombreux indices proposés auparavant, certains ne considèrent qu'un seul trait tandis que d'autres ne mesurent pas la diversité directement dans l'espace multidimensionnel. Ainsi, l’indice FD (Petchey & Gaston 2002) est mesuré le long d’un dendrogramme fonctionnel dérivé des distances interspécifiques observées dans l’espace multidimensionnel. Cette simplification du nombre de dimensions induit inévitablement une déformation par rapport à la répartition originale des espèces (Podani & Schmera 2007). Cette déformation varie suivant la méthodologie employée pour construire l’arbre (calcul des distances entre espèces et algorithme d’agglomération). Il est important de la prendre en compte puisque les valeurs de diversité fonctionnelle dépendent directement de la topologie de l’arbre. Pour répondre à cette limitation, nous avons développé une nouvelle méthodologie de construction de l’arbre (Manuscrit C). Elle vise à minimiser la déformation lors de la construction du dendrogramme. Pour cela toutes les méthodes de construction sont testées, seules ou en combinaisons. Au final, seul le meilleur arbre est conservé. Cette approche *ad hoc* limite donc les biais et elle permet en plus une évaluation objective de la qualité des dendrogrammes.

Nous avons aussi démontré que les autres indices de diversité étaient en fait redondants avec les trois indices présents dans le Manuscrit A. Il n’existe donc que trois facettes indépendantes pour capturer la diversité fonctionnelle (Manuscrit D). En particulier, l’indice FD apparaît très corrélé à l’indice de richesse fonctionnelle. En pratique, il est donc préférable d’utiliser l’indice de richesse directement défini dans l’espace multidimensionnel (volume de l’enveloppe convexe). Néanmoins, celui-ci n’est pas défini lorsque le nombre d’espèces est inférieur au nombre de traits. Il est alors utile de disposer d’un autre indice, tel le FD qui lui est utilisable même lorsque le nombre de traits dépasse le nombre d’espèces.

L’indice Q (Rao 1982), analogue à une entropie, apparait comme un indice synthétisant les trois composantes (avec toutefois une forte corrélation avec la richesse fonctionnelle). Cet indice tient compte à la fois des différences fonctionnelles entre espèces et de leurs abondances, et présente en plus l’avantage d’être concave. Nous l’avons donc utilisé pour décomposer la diversité et ainsi proposer un indice de diversité β fonctionnelle (Manuscrit E). Ce nouveau cadre d’étude est particulièrement adapté pour discriminer les mécanismes d’assemblage des communautés (filtres environnementaux, mécanismes neutres, dispersion).

7.1.3 De la composition des communautés au fonctionnement des écosystèmes : identité ou diversité fonctionnelle ?

Depuis les années 90, le débat s'est focalisé sur le fait de savoir si c'était la richesse spécifique ou la diversité fonctionnelle qui influençait les processus écosystémiques. Il ne fait plus de doute aujourd'hui que c'est la diversité fonctionnelle qui est décisive (cf. Petchey *et al.* 2004).

Un nouveau débat a néanmoins émergé pour savoir quelle facette de la structure fonctionnelle des communautés était prépondérante pour expliquer les processus écosystémiques. En effet, selon l'hypothèse du ratio de biomasse de Grime (1998), les espèces influencent les processus écosystémiques proportionnellement à leur biomasse. Par extension, en ne tenant compte que de la valeur agrégée d'un trait (moyenne pondérée par les abondances), il est donc possible de déterminer l'identité moyenne d'une communauté (Quested *et al.* 2007). Cette identité fonctionnelle moyenne d'une communauté a été liée avec succès aux niveaux de productivité primaire (Garnier *et al.* 2004) et fut donc considéré comme facteur explicatif majeur. Parallèlement, la diversité fonctionnelle des communautés est aussi décrite comme facteur explicatif majeur dans les processus écosystémiques (Petchey *et al.* 2004). A l'heure actuelle, il n'existe toujours pas de consensus sur la hiérarchie du pouvoir explicatif de ces deux composantes de la structure fonctionnelle des communautés (mais voir Mokany *et al.* 2008). Ceci est en partie dû au fait que jusqu'à présent il n'existait pas d'indices permettant de décrire optimalement la diversité fonctionnelle. Celle-ci peut désormais être caractérisée par ses trois facettes indépendantes (richesse, régularité et divergence). Ces indices pourront donc être comparés aux traits moyens des communautés pour analyser leurs pouvoirs explicatifs respectifs sur les processus et la stabilité des écosystèmes.

Il est donc nécessaire de poursuivre les études sur des communautés (végétales, animales, aquatiques et terrestres) et des processus contrastés (productivité, résistance à l'invasion,…). Il est en effet probable qu'il n'y ait pas une règle générale mais plutôt que les propriétés écosystémiques soit chacunes influencées par une ou plusieurs facettes. Ainsi, une forte richesse couplée à une forte régularité fonctionnelle devrait permettre une meilleure utilisation des ressources disponibles et donc une meilleure productivité. A l'inverse, une forte richesse et une forte divergence pourrait indiquer une vulnérabilité face à l'invasion d'espèces généralistes. En pratique, de telles analyses doivent être faites sans a priori, en testant simultanément le pouvoir explicatif des valeurs de traits agrégés et des différents indices de diversité fonctionnelle sur chaque processus écosystémique. Cela peut se faire via une régression multiple ou de manière plus intégrative à l'aide de modèles à équations structurées (Mokany *et al.* 2008).

7.2 Différences de réponse face aux variations des conditions environnementales

7.2.1 Une structure fonctionnelle stable malgré un fort gradient environnemental

Le premier axe d'étude de cette thèse était d'analyser la dynamique de la diversité fonctionnelle face à un gradient environnemental. Les résultats présentés au Chapitre 5 montrent clairement que la structure fonctionnelle et la structure trophique des communautés sont stables le long du fort gradient environnemental (Figure 7.1). Ce résultat est à mettre en regard de la forte dissimilarité dans la composition taxinomique des communautés le long de ce même gradient.

Cette forte dissimilarité taxinomique est à corréler à la forte variabilité des conditions abiotiques observée à Terminos, notamment en termes de salinité, qui agissent comme des filtres sur la portion du gradient que peut occuper chaque espèce. Néanmoins, la région étudiée est globalement marquée par une faible profondeur et une abondance de matière organique due aux apports de fluviaux. Cette relative homogénéité pourrait s'avérer en fait structurante pour les communautés. Nous avons en effet démontré la dominance de deux groupes fonctionnels « cœur », quelque que soit les variables environnementales. Cette dominance conjointe des espèces omnivores-détritivores (poissons-chats) et omnivores-carnivores (sciénidés) génère le faible « turnover » fonctionnel observé, chaque station présentant une biomasse équivalente pour chacun de ces deux groupes. Plus généralement, la structure trophique du necton montre elle aussi une stabilité le long du gradient environnemental en restant marquée par la dominance des espèces ayant un niveau trophique intermédiaire (3-3.5).

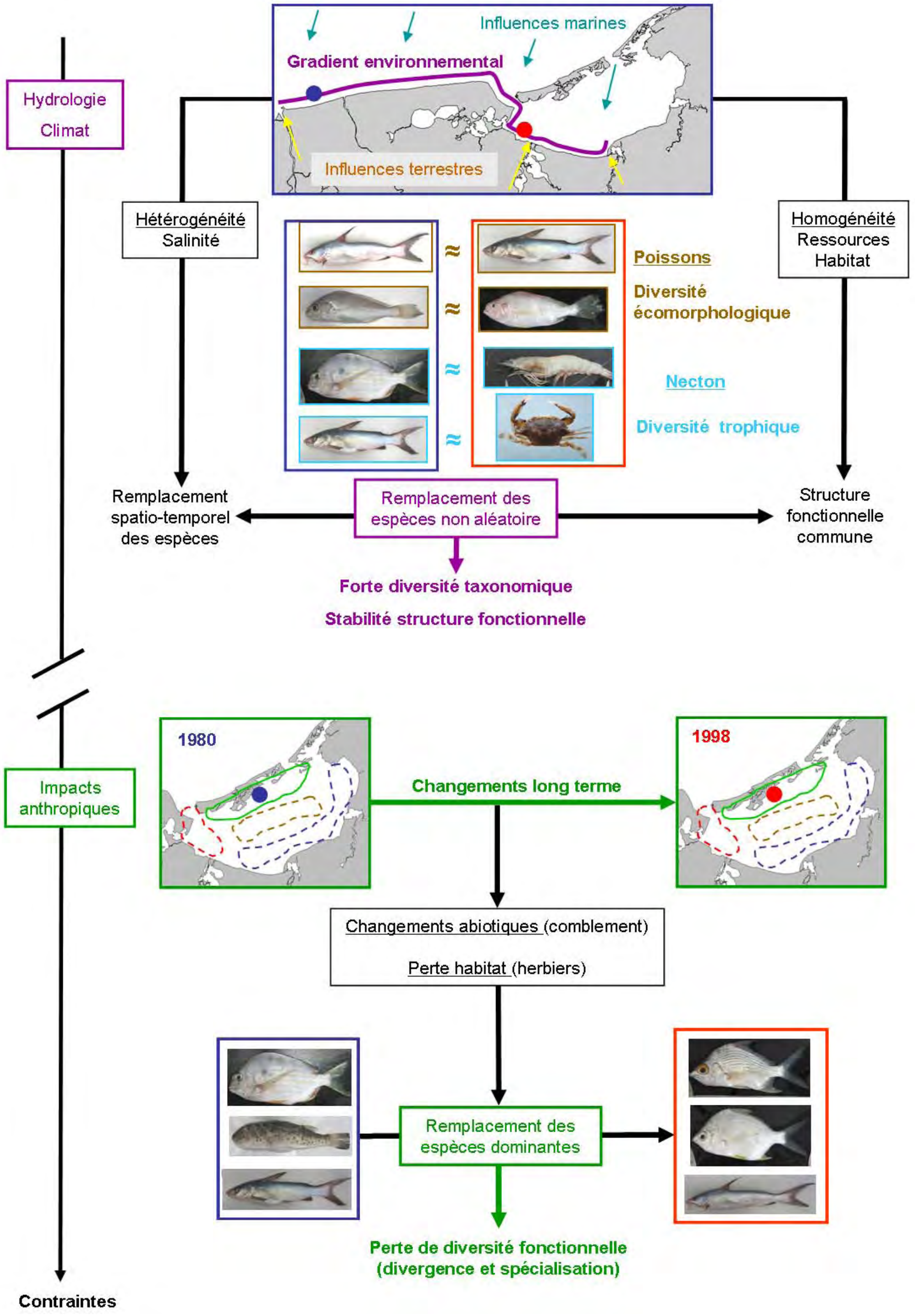


Figure 7.1. Schéma synthétique de la dynamique de la diversité fonctionnelle aux deux échelles d'étude.

En résumé, le remplacement des espèces le long du gradient environnemental n'est pas aléatoire mais se fait à l'intérieur des groupes fonctionnels (écomorphologiques ou trophiques) dominants. En d'autres termes, parmi les très nombreuses espèces présentes au niveau régional, seules celles passant le filtre lié aux conditions abiotiques peuvent être présentes dans une communauté donnée. Et parmi celles-ci seules les espèces favorisées par les ressources sont abondantes.

Ces conclusions méritent d'être comparées à des résultats obtenus pour d'autres écosystèmes. Par exemple, il est hautement probable que la structure fonctionnelle dans les écosystèmes oligotrophes soit aussi très stable dans l'espace et le temps. En effet, les ressources y sont limitées et le réseau trophique relativement simple et seules quelques stratégies fonctionnelles doivent être favorisées (ex : planctonivore, mangeurs de crustacés benthique, piscivore).

Des analyses similaires sur des producteurs primaires seraient particulièrement instructives pour voir si des habitats ayant les mêmes ressources (lumière, eau, minéraux) mais positionnés le long d'un gradient de stress (par exemple la température) produisent aussi une faible dissimilarité fonctionnelle.

7.2.2 Mais une perte de diversité fonctionnelle à long terme

Le deuxième axe d'étude visait à évaluer la dynamique de la diversité fonctionnelle à plus long terme et plus spécifiquement face aux perturbations d'origine anthropique survenues dans la lagune.

Dans le chapitre 6, nous avons ainsi mis en évidence une diminution significative de deux facettes de la structure fonctionnelle des communautés de poissons : la divergence fonctionnelle et la spécialisation fonctionnelle (Figure 7.1). Or cette perte est survenue dans les communautés les plus riches (en espèces et en biomasse) et dans un habitat singulier pour la région : les herbiers de phanérogames. Plus particulièrement, nous avons montré que le remplacement des espèces dominantes n'était pas aléatoire. Il correspond en effet à une perte des espèces inféodées aux herbiers et à une émergence d'espèces de type détritivore plutôt estuariennes. Or les espèces « perdantes » occupaient une portion externe du volume fonctionnel du fait de leur combinaison de traits particulière. A l'inverse, les espèces « gagnantes » ont des valeurs de traits plus moyennes et ne font donc qu'accentuer la dominance d'abondance au centre du volume fonctionnel.

Comme nous l'avons vu au paragraphe précédent la structure fonctionnelle est stable face à la variabilité des conditions abiotiques. Cependant ici le principal changement est beaucoup plus « profond » puisqu'il concerne l'habitat dans son ensemble (structure physique, ressources associées). Les modifications qu'il a subies ont donc perturbé profondément la structure des communautés en bouleversant les niches écologiques disponibles.

La description de la diversité fonctionnelle des communautés est donc particulièrement utile lorsqu'elle est menée à plusieurs échelles complémentaires. Ainsi, dans le cas d'étude présent, la démonstration de la stabilité observée dans la structure fonctionnelle face à un fort gradient environnemental et un fort turnover d'espèces, donne encore plus de poids à la mise en évidence d'une perte de diversité fonctionnelle à long terme.

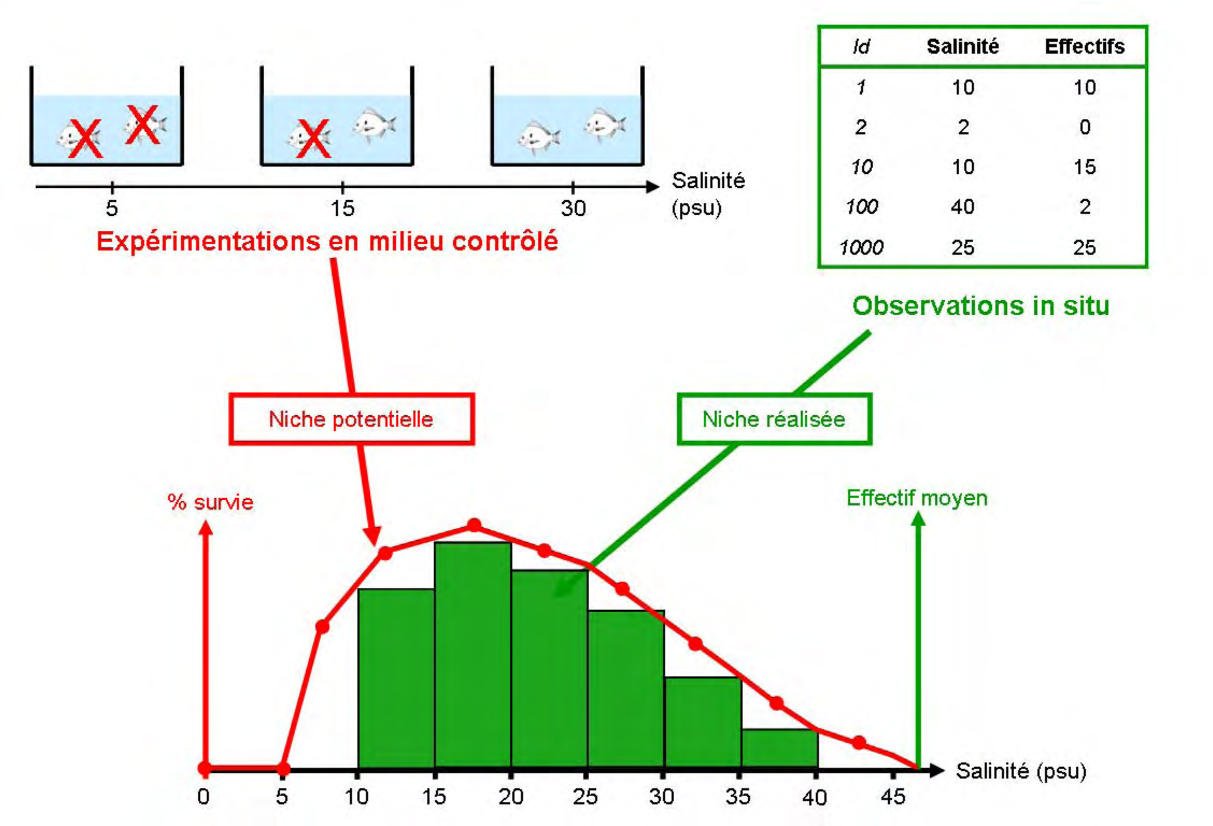
De telles approches multi-échelles devraient être tout particulièrement efficaces pour analyser la vulnérabilité des écosystèmes aux perturbations (ex : blanchiment sur les récifs coralliens). En effet, les indices de diversité fonctionnelle peuvent détecter la diminution de la dominance de certaines stratégies fonctionnelles (ex : les herbivores) jouant un rôle clé dans la résistance et la résilience face à la perturbation.

7.3 Perspectives

7.3.1 Quantifier la tolérance à la salinité : un besoin urgent en milieu estuarien

Dans le Manuscrit A nous avons présenté une approche fonctionnelle des poissons via l'utilisation de traits décrivant leurs fonctions biologiques principales. Dans les applications aux communautés de poissons (Chapitre 5 et 6), nous n'avons décrit que les fonctions liées à l'acquisition des ressources et à la locomotion et ce à l'aide de traits morpho-anatomiques. Or, les contraintes éco-physiologiques et tout particulièrement celles liées à la salinité jouent un rôle majeur dans la distribution des espèces. Il apparaît donc complémentaire de caractériser fonctionnellement la tolérance à la salinité, au moins pour les espèces les plus abondantes.

Ceci peut être fait de deux manières (Figure 7.2). Tout d'abord, il est possible de réaliser des études expérimentales sur la survie des individus soumis à différents niveaux de salinité. Ces approches sont toutefois longues et nécessitent des expérimentations en conditions contrôlées. En première approximation, il est néanmoins possible de tester simplement la survie à court terme des individus, même si l'idéal serait d'estimer la « fitness ». Cette approche expérimentale viserait à quantifier la niche potentielle d'une espèce.



Id	Salinité	Effectifs
1	10	10
2	2	0
10	10	15
100	40	2
1000	25	25

Figure 7.2. Illustrations des deux méthodes pour la quantification de la tolérance d'une espèce à la salinité. A gauche, l'approche expérimentale en conditions contrôlées fournissant le taux de survie pour les salinités testées. A droite, l'approche in situ utilisant des relevés écologiques pour en déduire l'effectif moyen présent dans chaque classe de salinité. La niche de l'espèce correspond à la distribution des effectifs (ou du taux de survie) le long du gradient de salinité. La niche potentielle en rouge est parfois plus large que la niche réalisée.

Au contraire, la deuxième méthode est indirecte et empirique. Elle consiste à évaluer la niche réalisée d'une espèce en utilisant les relevés écologiques de terrain. Dans le cas de la lagune de Terminos, nous avons à disposition plus d'un millier d'observations avec à chaque fois la salinité et l'abondance des espèces. De plus, ces données couvrent une très large gamme de salinité allant de 0 à 42 psu.

Pour chaque espèce il est donc possible d’évaluer la distribution de sa densité de population le long du gradient de salinité, discrétisé en plusieurs classes. Ceci doit bien entendu être effectué en standardisant par l’effort d’échantillonnage pour les différents niveaux de salinité. On obtient ainsi un nombre d’individus moyen pour chaque classe de salinité. Pour estimer l’abondance, il nous semble préférable de considérer le nombre d’individus plutôt que la biomasse, car le « choix » d’être présent dans un niveau de salinité est individuel. Cette distribution correspond à la niche réalisée de l’espèce sur ce gradient. En effet, il est tout à fait possible qu’une espèce supporte des salinités supérieures à 42psu. Toutefois de telles concentrations ne sont pas observées dans la zone d’étude, donc les occurrences de l’espèce ne pourront pas traduire une telle adaptation.

Pour les deux types d’estimation (expérimentation et observation in situ) on obtient donc une distribution d’abondance (ou de pourcentage de survie) le long d’un gradient de salinité. La tolérance à la salinité peut alors être décrite par deux indices complémentaires (Figure 7.3). Tout d’abord, la gamme de salinité occupée par une espèce peut être estimée soit de manière brute (maximum moins minimum toléré) soit via les quartiles ($3^{ème}$ – 1^{er} quartile). Par ailleurs, la régularité de l’occupation du gradient de salinité peut aussi être estimée (Mouillot *et al.* 2005a). Les valeurs de ces deux indices permettent de discriminer les espèces « spécialistes » des espèces « généralistes » (Figure 7.3). Les premières sont caractérisées par une survie (ou présence) dans une faible gamme de salinité tandis que les secondes tolèrent une large gamme avec des effectifs comparables pour les différentes classes de salinité.

Les notions de spécialiste et généraliste sont largement présentes dans la littérature mais ne font pas l’objet d’un consensus sémantique ou pratique. Une réflexion transversale a donc été menée en parallèle de cette thèse en collaboration avec d’autres équipes de recherche. Elle est présentée sous la forme d’un article de synthèse (Manuscrit I, Devictor *et al.*, *in prep*).

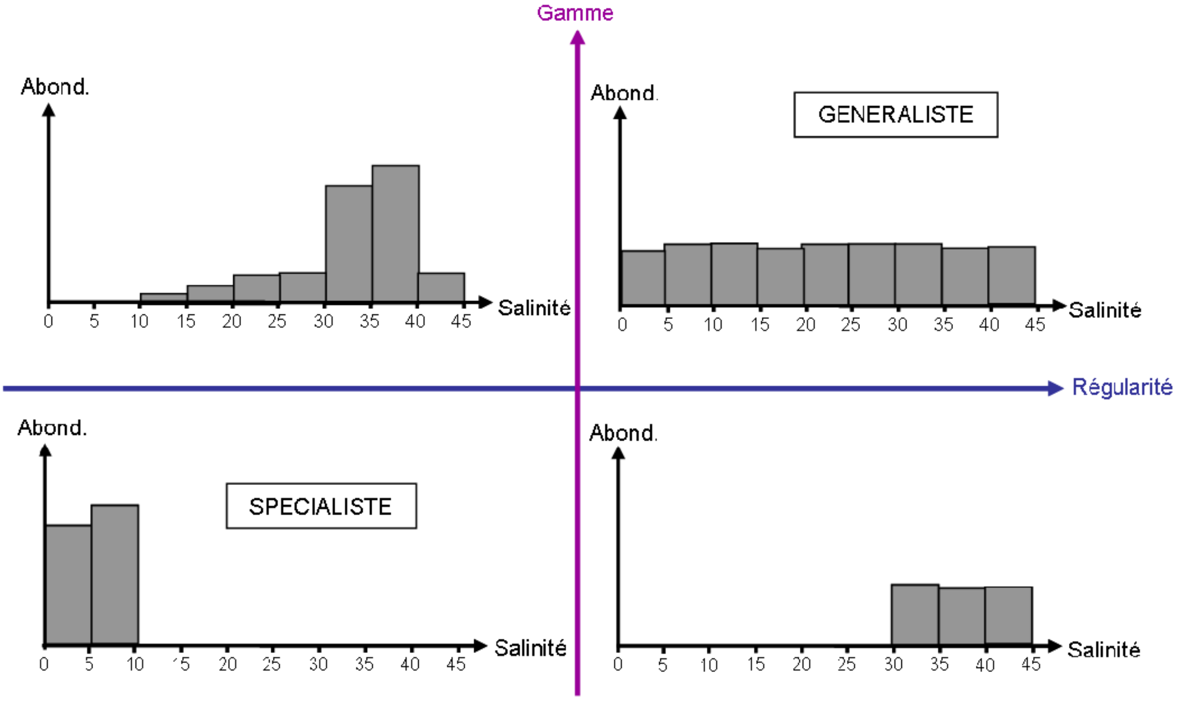


Figure 7.3. Patrons de tolérance à la salinité de quatre espèces hypothétiques ayant des niches contrastées en termes de gamme et de régularité d'occupation. Une espèce spécialiste est définie comme une espèce ayant une faible gamme et une forte irrégularité. A l'inverse, une espèce généraliste occupe une large gamme avec des effectifs identiques dans chacune des classes.

Les premières analyses menées en se basant sur la niche réalisée (salinité) des espèces de la lagune de Terminos ont permis de mettre en évidence de fortes différences interspécifiques. Ainsi, certaines espèces (ex : *Polydactylus octonemus*) montrent des profils typiquement marins en n'étant présentes que pour de fortes salinités (>35psu). D'autres ont des profils plus estuariens et occupent une large gamme de salinités avec soit une préférence pour les eaux faiblement salées (*Cathorops melanopus*) soit pour les eaux plus concentrées (*Bagre marinus*).

Par ailleurs, pour certaines espèces plutôt marines, les profils issus des observations de terrain montrent un effet seuil autour de 12 psu. Or ce seuil correspond à l'osmolarité du milieu interne des poissons téléostéens et donc à la limite entre hypo et hyper osmorégulation (Marshall & Grosell 2006). Ce changement dans le type d'osmorégulation est très contraignant physiologiquement car il nécessite une « inversion » des flux cellulaires.

De même, pour certaines espèces, la distribution est bimodale et pourrait en fait refléter des différences de capacités osmorégulatrices entre plusieurs stades de vies. En effet, la capacité à osmoréguler se développe avec l'âge (Varsamos *et al.* 2005) et par conséquent les juvéniles supportent une plage de salinité plus restreinte que les adultes.

Il serait donc intéressant de valider ses observations par des expérimentations en aquarium. En priorité, il serait utile de connaître les tolérances potentielles des espèces les plus abondantes et notamment celles des trois poissons-chats, à l'âge adulte mais aussi au stade juvénile. Les résultats permettront de comprendre le rôle proximal de la salinité dans la distribution spatio-temporelle de ces espèces.

7.3.2 Vers un modèle nul de partition de niche écologique

A l'aide d'estimateurs simples, nous avons pu mettre en évidence une partition de la gamme de salinité entre les trois espèces de poissons-chats. Ainsi, *Bagre marinus* est une espèce plutôt marine, *Ariopsis felis* est estuarienne avec une préférence pour les salinités intermédiaires et enfin *Cathorops melanopus* est aussi estuarienne mais avec une préférence pour les eaux à faible salinité. Ces premiers résultats pourraient être confirmés par des expérimentations simples comme décrit précédemment.

Plus généralement, dans le Manuscrit F, nous avons montré qu'il n'y avait pas de dominance absolue d'une espèce dans les deux groupes « cœurs » mais au contraire une complémentarité des espèces qui dominent successivement dans les communautés. Néanmoins, ces observations méritent d'être testées de manière plus approfondie et de manière plus générale. Dans cette perspective, nous proposons une analyse des relations entre la niche fonctionnelle et la niche environnementale des espèces (Figure 7.4).

Plus particulièrement, nous souhaitons tester si le chevauchement le long du gradient de salinité est corrélé à la ressemblance fonctionnelle. S'il existe une relation positive entre ces deux facettes de la niche, alors les espèces ayant des stratégies d'acquisition de la nourriture et/ou de locomotion similaires sont présentes dans les mêmes gammes de salinité. L'examen des abondances de chaque espèce peut alors fournir une estimation des capacités compétitrices de chaque espèce. A l'inverse, une corrélation significativement négative traduirait le fait que les espèces fonctionnellement proches se partagent le gradient de salinité et donc qu'elles n'entrent pas en compétition. Autrement dit, il y aurait une ségrégation environnementale (et donc spatiale) des espèces fonctionnellement proches. Une telle démonstration serait un argument en faveur de la notion de limitation de similarité évoquée par MacArthur & Levins (1967) mais qui n'a que rarement été observée.

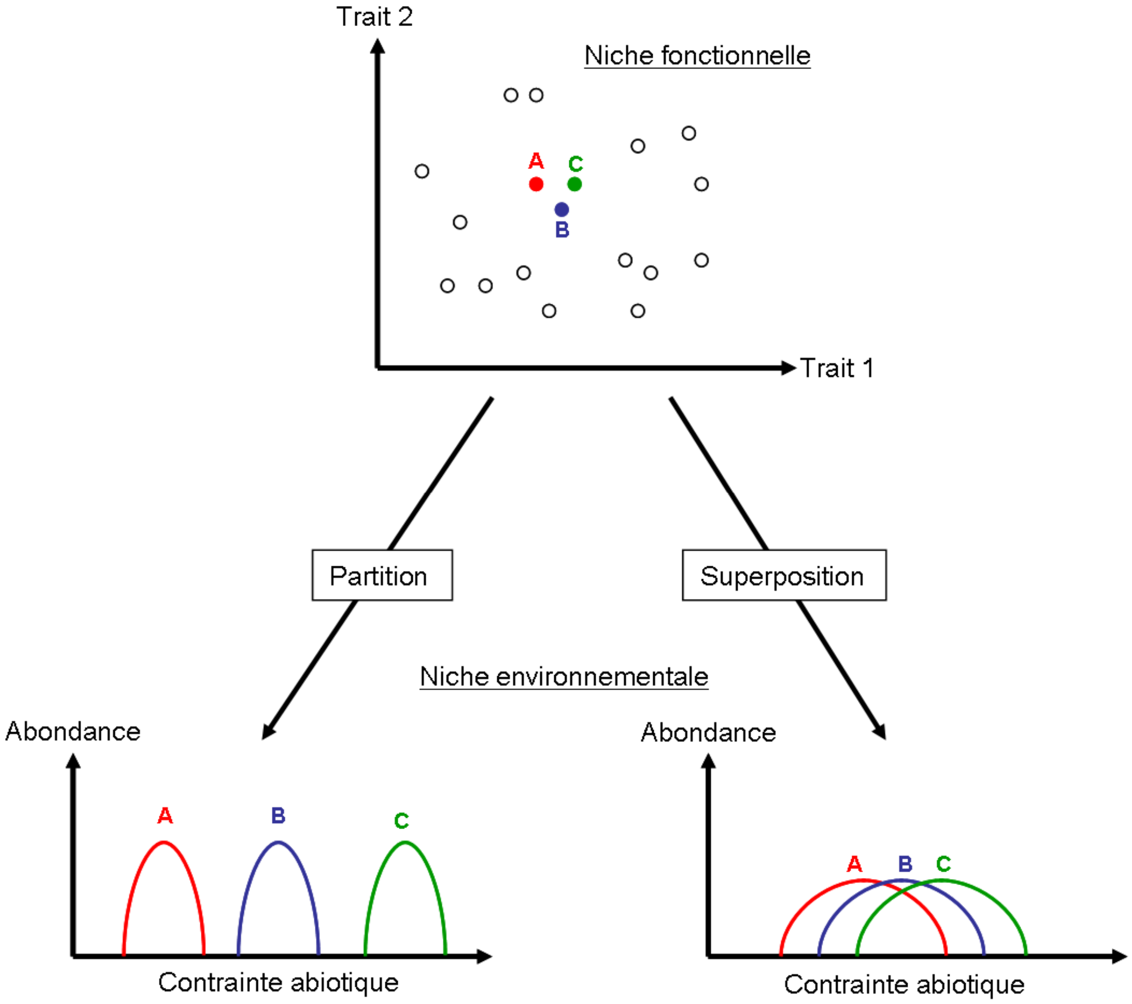


Figure 7.4. Représentation schématique des relations possibles entre niche fonctionnelle et niche environnementale. La niche fonctionnelle est décrite par des traits fonctionnels (ici deux). La niche environnementale peut être approximée par la distribution des abondances d'une espèce le long d'un gradient abiotique. Parmi un pool d'espèces, certaines sont fonctionnellement très proches les unes des autres (A, B et C). Elles peuvent avoir des niches environnementales similaires (droite) ou au contraire se partitionner l'ensemble du gradient (gauche).

En pratique, ce test peut être fait en testant la corrélation (test de Mantel) entre la matrice de distances issue des valeurs de traits fonctionnels et la matrice de dissimilarité des niches environnementales. Cette dernière est le complémentaire du chevauchement de niche le long du gradient de salinité (estimé à partir de la méthode des kernels, Mouillot *et al.* 2005b). Cette approche est globale puisqu'elle prend en compte toutes les espèces.

Il est aussi possible de mener de telles analyses à l'intérieur de chaque groupe fonctionnel (obtenu via une agglomération). Il suffit alors d'utiliser un modèle nul visant à tester si deux espèces appartenant à un même groupe ont un niveau de chevauchement de leurs niches environnementales significativement différent de celui de deux espèces prises au hasard.

7.3.4 Perte de diversité fonctionnelle et/ou homogénéisation biotique ?

Dans le contexte des changements globaux, le concept d'homogénéisation biotique a récemment émergé dans la littérature (McKinney & Lockwood 1999, Olden & Rooney 2006). Le terme d'homogénéisation traduit le fait que l'Homme favorise un certain nombre d'espèces en les introduisant dans de nombreux écosystèmes tandis qu'il contribue à en pénaliser d'autres, voire à les faire disparaitre. Par ailleurs, les espèces « perdantes » et « gagnantes » présentent des traits différents, relatifs à leur capacité à prospérer dans des environnements anthropisés. Par conséquent, les communautés sous pression anthropique tendent à se ressembler, du point de vue de leur composition mais aussi de leurs traits, donc fonctionnellement.

Pour la lagune de Terminos l'étude des changements biotiques et abiotiques à long terme a été menée pour des zones environnementales distinctes. Nous proposons, en perspective, de tester si la lagune, dans son ensemble, a subi une homogénéisation biotique, parallèlement à la perte de diversité fonctionnelle mise en évidence dans la zone marquée par les herbiers. Les changements observés suggèrent une homogénéisation puisque les nouvelles espèces dominantes semblent plus « lagunaires » comparées aux espèces initialement dominantes, qui elles étaient plus typiques des herbiers. Or la lagune est majoritairement sous influence estuarienne, notamment dans sa partie sud et ouest. Par conséquent, la disparition d'un habitat original et des espèces associées pourrait entraîner une homogénéisation des communautés de poissons à l'échelle de la lagune.

D'un point de vue pratique, la dissimilarité moyenne entre les communautés de poissons occupant les différentes zones peut être estimée grâce au cadre d'étude défini autour de la diversité β fonctionnelle. Il suffit alors de calculer cet indice pour les deux périodes (1980 et 1998) et de tester la différence observée dans la dissimilarité moyenne contre celles obtenues sous un modèle nul (similaire à celui employé dans le Manuscrit H). La baisse significative de dissimilarité moyenne entre 1980 et 1998 suggèrerait une homogénéisation fonctionnelle des communautés de poissons liée à l'homogénéisation des habitats locaux.

7.3.5 Des poissons au necton et du necton aux organismes aquatiques

Les poissons forment une unité fonctionnelle cohérente dans le sens où ils ont un plan d'organisation commun avec notamment un squelette interne, une symétrie latérale et des branchies. Nous avons ainsi proposé une liste de traits fonctionnels pour décrire les actinoptérygiens. En pratique, nous avons même étendu ces traits morpho-anatomiques aux chondrychthiens.

Le necton est quant à lui défini d'un point de vue strictement fonctionnel, en rapport avec la capacité locomotrice des organismes. Nous l'avons étudié en prenant comme indicateur le niveau trophique moyen. Même si ce dernier peut être vu comme un trait fonctionnel, il n'est pas réellement optimal car trop simplificateur. Il serait donc complémentaire de développer une méthodologie multi-traits pour l'ensemble des organismes nectoniques. Cette démarche est d'autant plus nécessaire qu'elle permettrait de prendre en compte les convergences évolutives remarquables au sein du necton. Ainsi, il y a plus de ressemblance fonctionnelle entre un calamar et un barracuda dans la manière de capturer les ressources, qu'entre un barracuda et une sole. En effet, le calamar et le barracuda vivent en pleine eau, ont un corps très allongé et une bonne vision en relation avec leur technique de chasse par accélération. La sole est par contre, très aplatie verticalement, possède des petits yeux et une petite bouche et vit sur le fond où elle fouit dans le sédiment pour trouver des invertébrés. De la même manière que pour les poissons, les traits fonctionnels visant à caractériser le necton dans son ensemble devront décrire l'acquisition des ressources, la locomotion, la protection vis-à-vis des prédateurs ou la tolérance aux stress environnementaux. Une telle démarche mérite d'être initiée.

Il serait aussi complémentaire de s'intéresser à la dynamique des populations, notamment de connaître l'âge à maturité et la fécondité moyenne. Ces paramètres sont en effet de bons indicateurs pour prévoir la sensibilité des espèces aux prélèvements par la pêche. En effet, même si la majorité de ces espèces ne sont pas directement ciblées, elles sont présentes en larges proportions dans les traits de chalut ciblant les crevettes.

Plus généralement, l'étude du fonctionnement des écosystèmes aquatiques nécessite l'intégration de tous les organismes vivants, donc non seulement le necton mais aussi les organismes planctoniques et, pour les écosystèmes peu profonds, les organismes benthiques. A titre d'exemple, il est clair que les méduses sont du point de vue de l'acquisition des ressources très similaires aux poissons planctonophages. De même, les oursins sont de redoutables brouteurs d'algues, comparables aux poissons perroquets des récifs coralliens.

Une telle approche fonctionnelle prenant en compte tous les organismes fait encore défaut, par comparaison avec les approches écosystémiques fondées sur les relations trophiques (ex : modèles ECOATH, Pauly *et al.* 2000). Il serait par exemple très intéressant d'analyser les différences et redondances fonctionnelles entre les différents compartiments et organismes, (ex : cycle des nutriments), afin de mieux évaluer les conséquences des changements abiotiques (ex : pollution organique) et biotiques (ex : surpêche d'une espèce) sur les communautés d'espèces, puis ensuite sur le fonctionnement des écosystèmes. Il semble évident que les changements au sein des communautés induits par les contraintes locales et globales ne sont pas sans effet sur les processus écosystémiques. Néanmoins, ces approches couplées font encore souvent défaut. Un tel projet à long terme, centré sur la question « Quelles communautés d'espèces suite aux changements abiotiques pour quel fonctionnement de l'écosystème ? » serait sûrement très porteur. Les outils de modélisation nous apparaissent comme la solution pour aborder de telles approches avec scénarios.

7.3.6 Quelle évolution depuis 10 ans ?

La perte de diversité mise en évidence dans la partie nord de la lagune est survenue en fait il y a plus de 10 ans. Depuis, il n'y a pas eu de nouvelle campagne d'échantillonnage à l'échelle de la lagune. Il serait donc très intéressant de renforcer la tendance observée ente 1980 et 1998 à l'aide de données plus récentes. Ces nouvelles données permettraient notamment de voir si les changements environnementaux se sont accélérés ou non, notamment le comblement de la lagune.

Par ailleurs, au vu des résultats concernant la zone nord de la lagune, il semble primordial de réaliser un état des lieux des herbiers de phanérogames. En effet, il n'y en a pas eu depuis les relevés originaux menés par Yáñez-Arancibia en 1980. Ainsi, seules des données parcellaires et des observations qualitatives sont disponibles pour les années suivantes.

En terme biologique, le premier indicateur à analyser est la biomasse totale. Elle peut être vue comme synthétisant la capacité biotique du milieu et les effets négatifs des prélèvements par la pêche. Il est donc primordial de voir si la sévère chute observée s'est prolongée ou si la biomasse totale s'est stabilisée.

Toutefois, la principale tendance à confirmer est la perte de divergence et de spécialisation fonctionnelle des communautés de poissons. Plus exactement, il est légitime de se demander si la forte diminution des espèces dominantes, plutôt spécialistes, n’est pas un signe précurseur de leur disparition. Dans cette hypothèse, la diminution se traduirait alors au niveau de la richesse fonctionnelle (Figure 7.5). Par ailleurs, il n’est pas impossible que les espèces dominantes en 1998 aient à leur tour été remplacées par d’autres espèces.

Du point de vue du necton, et notamment des crevettes, un changement dans leur distribution est observé dans la lagune depuis quelques années (Ramos-Miranda, comm. pers.). En effet, les crevettes rentrent de plus en plus profondément dans la partie sud ouest de la lagune par rapport aux années 90 (Ramos-Miranda, comm. pers.). Il serait donc intéressant de comparer l’évolution de la structure trophique du necton entre ces périodes pour voir si les crevettes ont remplacé une autre espèce de même niveau trophique, ou si au contraire leur présence traduit une modification de la structure trophique de cette portion de la lagune.

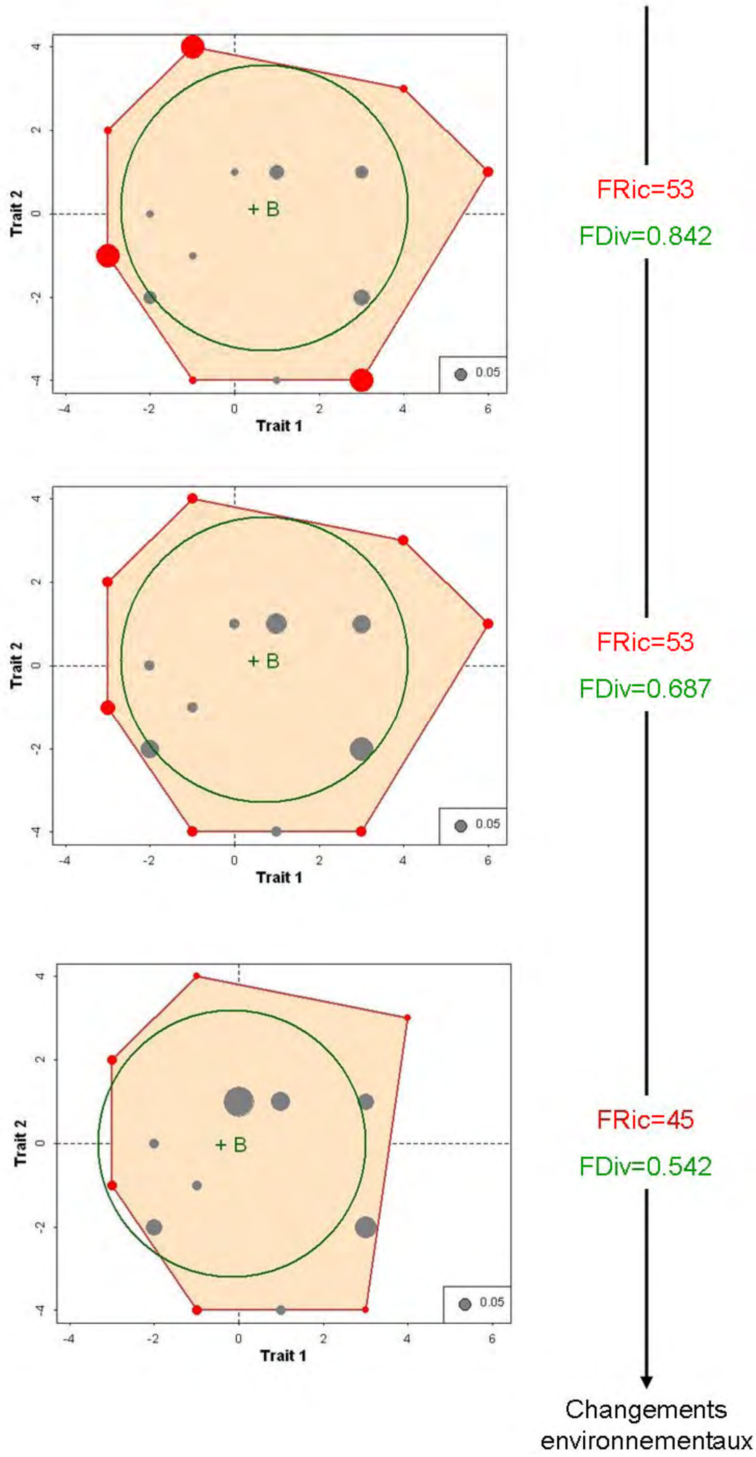


Figure 7.5. Dynamique de la diversité fonctionnelle d'une communauté hypothétique. Seuls deux traits sont considérés. Les espèces (points) sont placées dans l'espace fonctionnel en fonction de leur valeur de traits. Leurs abondances respectives sont proportionnelles à la taille des points. La richesse fonctionnelle est représentée en rouge (vertices, enveloppe convexe et surface) et la divergence en vert (barycentre, distance moyenne au barycentre). Au départ (T0), la divergence est élevée. Face aux changements environnementaux les espèces spécialistes diminuent et par conséquent la divergence aussi (T1). La richesse n'est pas affectée tant qu'une des espèces « extrêmes » n'a pas disparu (T 2).

7.3.7 Quelles conséquences pour le fonctionnement des écosystèmes et les services écosystémiques ?

La diversité fonctionnelle n'est en réalité qu'un outil conceptuel pour décrire une facette de la biodiversité et lier les communautés aux processus écosystémiques. A travers notre approche centrée sur les traits morpho-anatomiques, nous avons mis en évidence une perte de diversité fonctionnelle dans une des zones clés de la lagune de Terminos. Pour aller plus loin il faudrait donc quantifier les effets de la diversité fonctionnelle sur les processus et services écosystémiques effectués par les poissons.

Comme nous l'avons mentionné dans le Manuscrit A, les poissons participent et contrôlent les flux de matière. Néanmoins, ces processus écosystémiques ne sont pas faciles à décrire in situ pour une communauté donnée. Ainsi, il est difficile d'estimer en quoi les espèces présentes dans les herbiers de la lagune régulent la chaine trophique et le cycle des nutriments.

Cependant, pour certains processus, caractériser l'impact d'une espèce de poisson est envisageable. Ainsi, dans des eaux claires, il est possible d'observer (directement ou en filmant) des individus, par exemple lorsqu'ils broutent des algues (Bellwood *et al.* 2006a) ou du corail mort (Bellwood *et al.* 2003) et d'estimer ainsi leur impact sur le milieu (contrôle des macrophytes, bioérosion). Similairement, il est possible d'estimer l'excrétion d'azote et de phosphore d'un individu (McIntyre *et al.* 2008). Cette excrétion peut ensuite être intégrée au niveau écosystémique lorsque la structure des communautés (espèces et leurs abondances) est connue. Ces exemples demeurent toutefois très limités et de telles méthodes ne sont souvent pas généralisables.

Mettre en évidence le rôle des assemblages d'espèces est donc techniquement plus difficile. Ceci peut être fait de manière indirecte par le biais d'analyses statistiques visant à montrer les corrélations entre un processus écosystémique et une certaine composition en espèces ou un certain niveau de diversité. Néanmoins de telles approches sont souvent perturbées par la présence de facteurs cachés inhérents aux observations in situ.

En pratique, il est donc préférable de faire des expérimentations visant à contrôler les communautés. Il est alors possible de tester l'influence de la composition, en particulier fonctionnelle, sur les processus écosystémiques. Cette approche indirecte, consiste souvent en l'exclusion d'une ou quelques espèces d'une portion de l'écosystème. Ainsi, McIntyre *et al.*

(2007) ont prouvé le rôle prépondérant de quelques espèces détritivores sur la rétention de matière organique, et par conséquent la prévention de l'eutrophisation du milieu. De même, en excluant les espèces herbivores, Hughes *et al* (2007) ont démontré leur contribution à la résilience des récifs coralliens face aux épisodes de blanchiment. De telles approches expérimentales sont encore récentes du fait de leur coût et des contraintes techniques. Cependant leur rôle est décisif dans la compréhension des mécanismes écologiques.

Les services écosystémiques directs comme la provision alimentaire sont plus faciles à quantifier. Ainsi, il serait intéressant de corréler les changements de diversité fonctionnelle observés et l'évolution des captures par les pêcheurs en tonnage et en valeur marchande. Nous avons en effet montré une diminution significative de la biomasse totale mais aussi de la taille moyenne de certaines espèces. Plus généralement, les effets de la perte d'un habitat localisé peuvent donc se faire ressentir à une échelle bien plus importante que sa distribution. En effet, les espèces vivant dans la lagune servent de proies aux prédateurs côtiers lorsqu'ils entrent dans la lagune ou lorsque ces proies émigrent vers la zone côtière. De nombreuses espèces utilisent aussi la lagune comme nurserie ou comme zone d'alimentation saisonnière.

L'effet trophique à large échelle de la lagune et plus largement des apports fluviaux pourrait être étudié grâce à des marqueurs isotopiques. Il serait ainsi possible de quantifier l'influence de ces apports de matière tout au long de la chaine trophique (Darnaude *et al.* 2004, Darnaude 2005).

7.3.8 Vers une écologie fonctionnelle prédictive

La première étape en écologie est d'analyser les patrons. Puis à partir de ces observations, d'inférer la nature des mécanismes les ayant produits. Néanmoins, si ces deux étapes sont décisives pour la compréhension du monde qui nous entoure, il est encore plus stimulant d'essayer de prédire l'évolution des systèmes écologiques. Cette prévision doit permettre une anticipation des changements à venir et encourager la prévention de leurs effets.

L'écologie fonctionnelle des communautés, de par sa position à l'interface entre l'environnement et le fonctionnement des écosystèmes, offre de nombreux atouts dans une telle perspective (Figure 7.6). Il est donc souhaitable à terme de développer des modèles mécanistes efficaces utilisant les traits fonctionnels et visant à relier, par l'intermédiaire des traits des espèces, l'effet des changements globaux sur le fonctionnement des écosystèmes

(Lavorel & Garnier 2002). Dans un premier temps, il est nécessaire de prédire quelles stratégies fonctionnelles sont les plus vulnérables face à une perturbation donnée. Dans un second temps, l'intégration de ces résultats permettra de modéliser l'évolution de la structure des communautés. Finalement, la diversité fonctionnelle résultante servira de prédicateur pour quantifier les changements en termes de processus écosystémiques. Ces modèles nécessitent donc au préalable des études approfondies pour paramétrer les effets de l'environnement sur la composition des communautés et d'autre part l'effet des communautés sur les processus écosystémiques. Néanmoins, de tels modèles, une fois opérationnels, devraient se révéler décisifs pour prévenir les changements écologiques brutaux et souvent irréversibles dus à la disparition de quelques stratégies fonctionnelles clés.

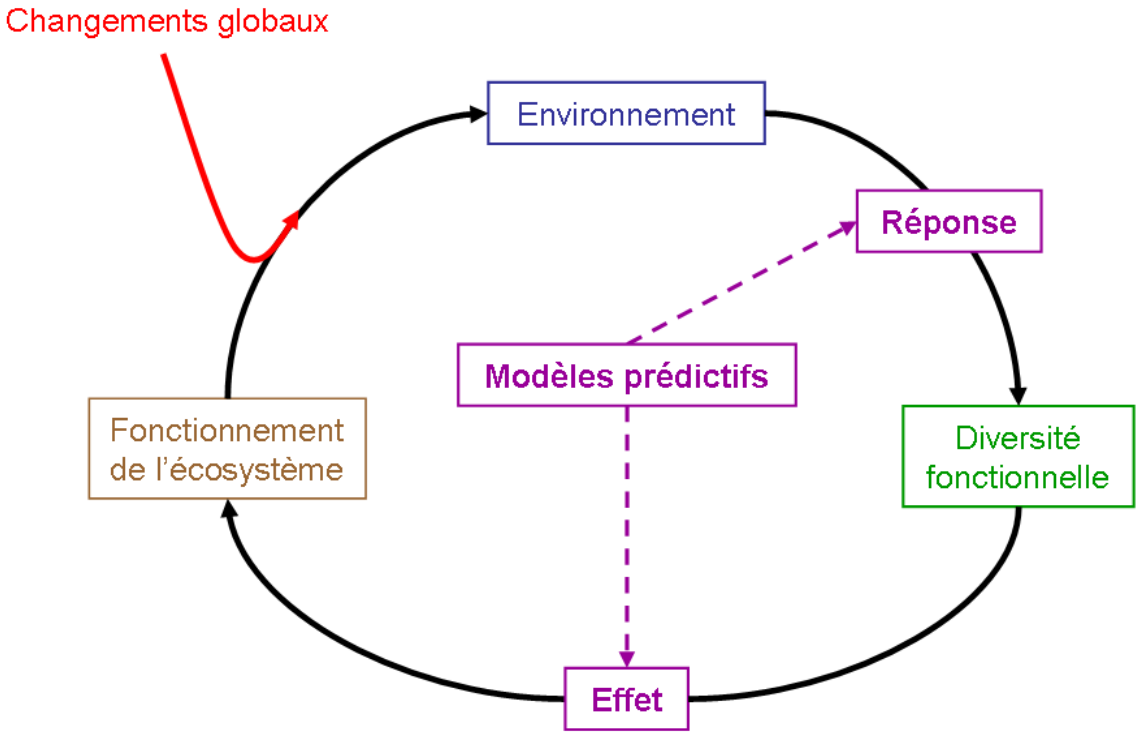


Figure 7.6. Schéma du rôle de la diversité fonctionnelle dans la prédiction de l'effet des changements globaux sur le fonctionnement des écosystèmes. Deux types de modèles prédictifs doivent être paramétrés : d'une part pour expliquer comment la diversité fonctionnelle répond aux conditions environnementales et d'autre part comment la diversité fonctionnelle affecte le fonctionnement des écosystèmes. La diversité fonctionnelle est à considérer au sens large, c'est-à-dire regroupant la présence d'espèces « ingénieurs », les valeurs de traits agrégés, ses différentes facettes (richesse, régularité, divergence, spécialisation) et sa structure inter-communautés (diversité β).

MANUSCRIT I

Toward a general framework for ecological specialization

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En préparation

Abstract

Ecological specialization is among the most popular concept in ecology. Various definitions and many metrics have been extensively used to characterize ecological specialization for several decades. More recently, the concept of specialization has been increasingly used by empirical studies investigating whether specialist and generalist species are equally at risk when facing global changes. However, comparison across studies is difficult because definition and measures of ecological specialization have become highly context and scale-dependent. It thus should be of general interest to propose a common agenda for studying ecological specialization both from theoretical and applied perspectives. Here, we propose a general framework for ecological specialization which allows a better understanding of various aspect of this concept. This framework highlights that i) ecological specialization implicitly refers to how a species respond to (Grinnellian-specialization), or impact (Eltonian-specialization) its environment; ii) that realized specialization derived from field data must be discerned from fundamental specialization measured from controlled experiment, and iii) that specialization can be defined and measured across spatial and temporal scales, and from individuals to communities. Finally, based on this framework, we propose original research directions to study the cause and consequences of ecological specialization.

Keywords: Ecological niche, Elton, Grinnell, Niche breath, Specialist-generalist, metrics

Introduction

Specialist species have been recently shown to be more declining and to experience higher extinction risk than generalists (primates, Harcourt et al. 2002; marsupials, Fisher et al. 2003; carabid beetles, Kotze and O'Hara 2003; plants, Rooney et al. 2004; bumblebees, Goulson et al. 2005; birds, Jiguet et al. 2007; butterflies, Polus et al. 2007; dung beetles, Horgan 2007; coral reef fish, Feary 2007; bats, Boyles & Storm 2007; butterflies, Wilson et al. 2008). Specialists are even considered to be the "great losers" of past and current global changes (McKinney 1997; Broennimann et al. 2006, Jiguet et al. 2007) so that their trend is used as indicators of unsustainable development at national and international scales (e.g., farmland-bird specialist indicator, Gregory et al. 2005).

In this context, a growing number of specialization indices have been proposed. For instance, inferring ecological specialization from species distribution is now widely used in macroecology (Calenge & Basille 2008). Alternatively, very detailed measures of dietary-specialization have highlighted that not only species, but also individuals, are more or less specialized (Bolnick et al. 2007). Ecological specialization has thus become highly dependent on the data, the scale or the ecological mechanism of interest, so that this concept is now most often redefined each time it is used (Ferry-Graham et al. 2002).

While the interest for specialization has grown strongly during the last decade, the concept of specialist and generalist species has a long history in ecology (Kassen 2002). In the theoretical literature, ecological specialization was most often considered as the ecological niche breath, resulting from evolutionary trade-offs between the ability of species to exploit a range of resources and their capacity to use each one (the "jack-of-all-trades is master of none" hypothesis; McArthur 1972). Specialization has early been shown to be a key attribute to predict the fate of species in heterogeneous environment (Levins, 1962) and many metrics were also early proposed to differentiate specialist from generalist species (Colwell and Futuyma, 1971, Petraitis, 1979).

Following this pioneer literature, the concept of ecological specialization was shown to deserve clarifications. In particular, in their review of ecological specialization, Futuyma and Moreno (1988) have emphasized the need to clarify specialization from the classical distinction between the fundamental niche of a species and its realized niche. Indeed, if this distinction is not made, a species which only use a subset of the available resources because of competitive exclusion will be considered to be specialized, although the species is potentially able to use a broader breadth of resource. Similarly, Pulliam (2000) has stressed the need to account for dispersal processes when measuring niche breath. Indeed, species might be found in unsuitable habitat because of source-sink dynamics or absent from suitable habitat because of dispersal limitation. Finally, Ferry-Graham et al. (2002) have also underlined the value of discerning ecological specialization (the range of resource used), mechanical specialization (encompassing physiological, morphological and behavioral constraint leading to specialization) and evolutionary specialization (the adaptative process leading to specialization).

Despite these clarifications, a general framework for ecological specialization and its related metrics is still missing and still a challenge of interest (Kearney 2006; Araújo & Guisan 2006). Indeed, the term specialization is now used inconsistently throughout the ecological literature for different biological level (individual, species, population or community) and measured at very different spatial scales. These disparities induce several confusions impairing to draw consistent inferences about ecological processes. For instance, if species response to disturbance is measured at different spatial scales or locations, disentangling true difference in disturbance effect from difference in the specialization level can be hazardous. Moreover, there is a growing need to assess the breadth of species niche to make relevant projection of future species distributions in response to global changes (Thuiller et al. 2008). In this respect, the need to clarify the relationship between the ecological niche theory and species distribution (either derived from niche modeling or habitat-suitability models) has been recently emphasized (Guisan and Thuillier 2005; Kearney 2006; Soberon 2007; Hirzel & Lay 2008). Third, specialization is often considered to be a species characteristic of conservation interest which can provide indicators of species or community response to land-use changes (Purvis et al. 2000; Devictor and Robert 2008; Filippi-Codaccioni et al. 2008). Consistency of how specialization is defined and measured should strengthen the robustness of these indicators and ensure their relevance when measured in a wide array of context and taxonomic groups.

Here, we develop a three-component framework to i) set a consensual definition for ecological specialization from the lowest common denominator of numerous existing definitions, ii) to identify why and how specialization should be scaled across spatial and temporal scales and from individuals to community and iii) to build a comprehensive tool-box for measuring ecological specialization depending on the data available and the question being asked. We finally use this framework to highlight future research directions that tackle problems related to specialization from innovative (yet realistic) angles.

A consensual definition of ecological specialization

Ecological specialization is most often defined as the ecological niche breath (or width) of a given species (Futuyma and Moreno 1988). As such, it should benefit from recent clarifications of the niche concept which have emphasized the need to discern the *Grinnellian* from the *Eltonian* dimension of the niche (Leibold 1995; Chase and Leibold 2003; Guisan & Thuillier 2005; Soberon et al. 2007). The Grinnellian niche describes the response of species to a given set of variables taken as resources (Grinnell 1917). It can be further extended to the traditional Hutchinson's (1957) concept of the ecological niche (which has been the most influential) if every biotic and abiotic resources are considered. In this case, the niche is more generally defined as a hyper-volume in the multidimensional space of ecological variables, within which a species can maintain a viable population (Hutchinson 1957). The Eltonian niche (sometimes called functional or trophic-niche, Silvertown et al. 2004) focuses on the impact of species in the environment rather than on its response to particular resources (Elton 1927). In other words, the Eltonian niche describes the species' "place in the community to which it belongs, either through explicit species-species interactions (e;g., number of prey) or through its implicit functional roles (e.g., decomposition rate). For instance, Rosenfeld (2002) measured the functional niche as the area occupied by a species in an n-dimensional functional space, measured as the species position along axis embodying functional attributes or process rates, rather than resource variables. Interestingly, this functional conception of the ecological niche has recently received new theoretical and methodological attention following the growing interest for functional traits in community ecology (McGill et al. 2006, Kearney & Porter 2006).

Based on this first distinction between the two classes of the ecological niche, we define the *Grinnellian-specialization* of a species as the variance in species' performance across a range of a given environment, broadly defined by one or several biotic (and/or abiotic) resources (Fig. 1a). Note that Grinnellian-specialization can be defined as the breath of species requirement using the term "resource" in its largest acceptation. For instance, Grinnellian-specialization include habitat-specialization when habitat is not solely considered as the physical place were the species occur but as influencing, somehow, species performance (e.g., species might need specific habitat for reproduction places, refugees for predators, specific food requirements, etc.).

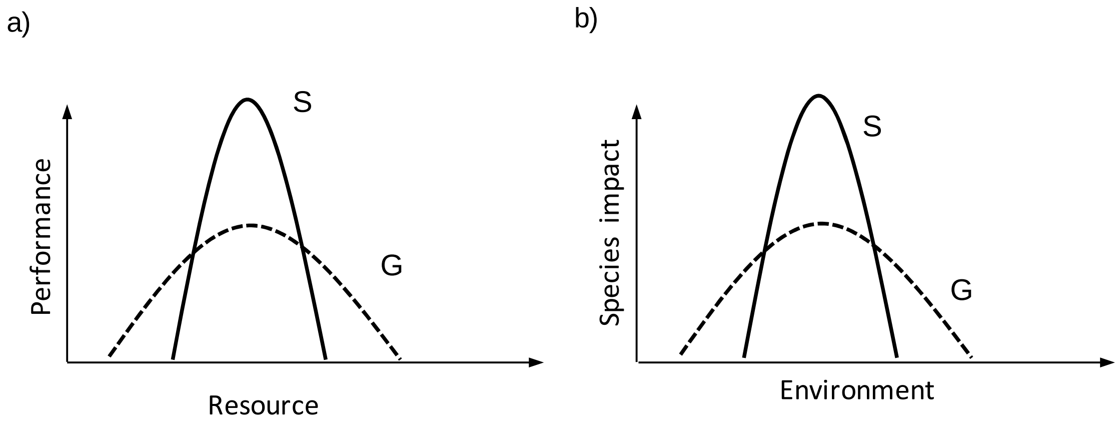

Figure 1. Definition of Grinnellian versus Eltonian specialization

a) The Grinnellian-specialization of a given species can be described by its variance in performance across a range of a given set of resources. For a given mean performance along a given resource, the dashed line describes the performance of a more generalist species (Generalist G) than the solid line (Specialist S). b) Eltonian specialization is defined as variance in the species impact on the environment. For a given mean impact, the species impact can be distributed through a large breadth of the environment (Generalist) or more restricted (Specialist)

The *Eltonian-specialization* refers to the functional place of the species in its environment and is measured as the species breath of function (that we assume to be synonym of impact or role) instead of resource used (Fig. 1b). Although Elton historically focused on the niche of a species as its place within the food chain (in terms of what the species eats), we use Eltonian-specialization to designate the breath of function involving explicit biotic interactions (e.g., pollination, predation) or abiotic impacts (e.g., oxygene generation, carbon dioxide production) or both. In other words, our definition of Grinnellian versus Eltonian-specialization only emphasizes that Eltonian-specialization is measuring the breath of effects of the species on the environment while the Grinnellian specialization reflects the breath of the species' requirement. Therefore, this distinction do not a priori depends on the particular variable, scale or data used.

The distinction between the Eltonian and Grinnellian-specialization is somewhat artificial (e.g., whether interacting with a resource is considered as a species requirement or a species impact depends on the question being asked), and not mutually exclusive (a Grinnellian-specialist may be an Eltonian-generalist or an Eltonian-specialist). However, this division sets a useful heuristic basis which includes most specialization definitions. Indeed, this distinction is found implicitly throughout the ecological literature on specialization. For instance, by tracking the evolution of species performance in a given environmental gradient under different selective pressures, evolutionary-ecologists working on species adaptation to varying environment have investigated evolution of Grinnellian-specialization (Levins 1962, Holt and Gaines 1992, Kassen 2002, Kawecki & Ebert 2004). Conversely, an extensive literature has focused on specialization vs. generalization in terms of the identity and number of interactions between species (e.g., predator and prey, pollinators and plants) focusing in this case on the Eltonian-specialization (Blüthgen 2006, Petanidou et al. 2008, Sargeant and Ackerly 2008).

The specialization concept can also be further clarified using the seminal distinction between the fundamental and realized niche (Hutchinson 1957). Indeed, both Grinnellian and Eltonian-specialization can be measured as an intrinsic species attribute (fundamental), or as a contingent property dependent on co-occurring species (realized). For instance, as realized-specialization is dependent on the presence of other species, studies that describe specialization as a species attribute by analyzing one specific community (site) may be biased or even misleading (Entling 2007). Moreover, if no distinction is made between realized and fundamental specialization, disentangling specialization resulting from true local adaptations to apparent specialization resulting from competitive exclusion and/or source-sink dynamics becomes unclear (Pulliam 2000). Separating realized from fundamental specialization is also useful to clarify niche metrics derived from niche modeling. Indeed, specialization metrics derived from correlative approaches based on the distribution of the organism implicitly incorporates many biotic interactions and abiotic constraints, and should thus be considered as a measure of the realized specialization (Kearney 2006).

Here, we simply define fundamental Grinnellian-specialization as the niche breath of the species, calculated after excluding any extrinsic biotic and abiotic factors that determine its realization (competition, predation, facilitation, or dispersal constraint). Fundamental Grinnellian specialization is thus generally derived from controlled experiment. Similarly, fundamental Eltonian specialization is the Eltonian niche breath inferred from species characteristics influencing species impacts (i.e., functional and morphological traits) rather than directly from their expression in the field. Any other measure of specialization (either Grinnellian or Eltonian) which is dependent on the presence or absence of other species, reflect the realized specialization.

The two axes (Grinnellian versus Eltonian and realized versus fundamental) must be seen as the limits of a continuum (Fig. 2). For instance, assessing the trophic role of a given species using the breath of its prey items will reflect the realized-Eltonian specialization (Fig 2a) (e.g., the analysis of stomach content of the black-browed albatross, *Thalassarche melanophrisalbatross* reflects its realized-Eltonian specialization on crustaceans, cephalopods and fish, Petry et al. 2007). Measuring the functional traits (e.g., morphology or behavior) of that species to determine its potential breath of resource used would reflect the fundamental Eltonian-specialization (Fig 2b) For instance, the longer and thinner bills are an adaptation for consuming more invertebrates and fewer seeds than other species (Grenier & Greenberg 2005).

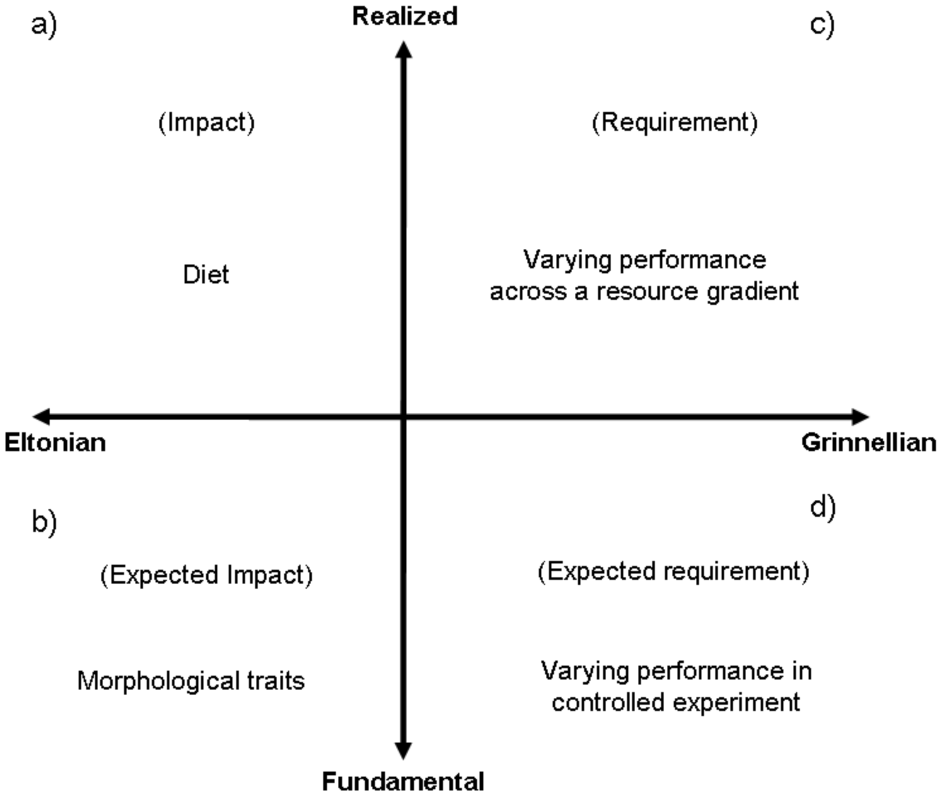

Figure 2. The lowest common denominator of ecological specialization**.** Most definition of ecological specialization implicitly refers to a specific conception of the niche (horizontal axis), which can be usefully separated in Eltonian and Grinnellian classes. Then, ecological specialization can be considered as realized or potential if measured with or without considering dispersal constraint and biotic interactions (vertical axis). These two axis delimitate respectively a) the Realized Eltonian-specialization; b) the fundamental Eltonian-specialization; c) the realized Grinnellian-specialization and d) the fundamental Grinnellian-specialization. In each case, an example of how specialization is generally measured is given in italic.

Similarly, investigating the variance in species performance along different resource (or habitat) types measured in the field (i.e., including all biotic interactions and dispersal constraint) would reflect a realized-Grinnellian specialization (Fig 2c), while measuring species performance in several conditions after excluding all between-species interactions and dispersal constraint would reflect the fundamental Grinnellian-specialization (Fig 2d) (e.g., the specialization to soil water availability in oaks, *Quercus sp,* measured under controlled moisture regime, and excluding other constraints, Poulos et al. 2007) .

Regardless the particular definition of ecological specialization considered, the great flexibility of this concept has also lead to define and measure specialization at various spatial, temporal and ecological levels. To be useful, our proposed classification of ecological specialization must thus be robust across these variations.

Ecological specialization across spatial, temporal and ecological scales

Spatial and temporal dependence of ecological specialization

The Grinnellian (or Eltonian) specialization is always implicitly conditioned on a selected set of resources (or type of impact), and on the spatial and temporal scale they are characterized. For instance, on a continental scale, some insects might be called specialists because they eat plants only within one genus. On the smaller scale of their geographical ranges, the same species could be considered generalists because they feed on numerous species of that genus (Fox and Morrow 1981). Similarly, Eltonian or Grinnellian specialization of a given species measured during a given time-period may only reflect a subsample of what condition the species can experience during a longer time-period. The definition and measure of specialization should thus be scaled across space and time. Surprisingly, although this problem of scaling is recurrent and inherent to any ecological pattern and process (Levins 1992, Wiens 1989), specialization have most always been treated and quantified as insensitive to differences in temporal and spatial scales, so that species are most often simply categorized as specialist or not (Berenbaum, 1996).

The spatial and/or temporal scaling of ecological specialization can shed light on important ecological processes and methodological problems. In this respect, Levins (1962) has early shown that the fate of specialist species is highly dependent on whether environmental fluctuations are occurring at high frequency (fine grained) and at low frequency (coarse grained). In particular, if the state of the environmental conditions experienced by an organism is constant relatively to its lifetime (coarse grain fluctuations), Grinnellian-specialization should be favored and maintained (Levins 1968). This difference in environmental grain should also influence Eltonian-specialization as the scale of environmental variation can lead to differences in which functional traits are affected (Engelmann and Schlichting 2005). These predictions can be tested only when the scale and/or locations at which specialization is measured are appropriately defined.

In fact, both Grinnellian and Eltonian-specialization may be constant across locations (Fig. 3a) or be influenced by true shift in niche breath induced by local adaptations (Fig 3b). For instance, according to the latitude-niche breadth hypothesis (McArthur, 1972) one expects greater specialization in the Tropics as species should experience a more predictable environment in lower latitudes (Vazquez and Stevens 2004;; Morin and Chuine 2006 ; Krasnov et al. 2007).

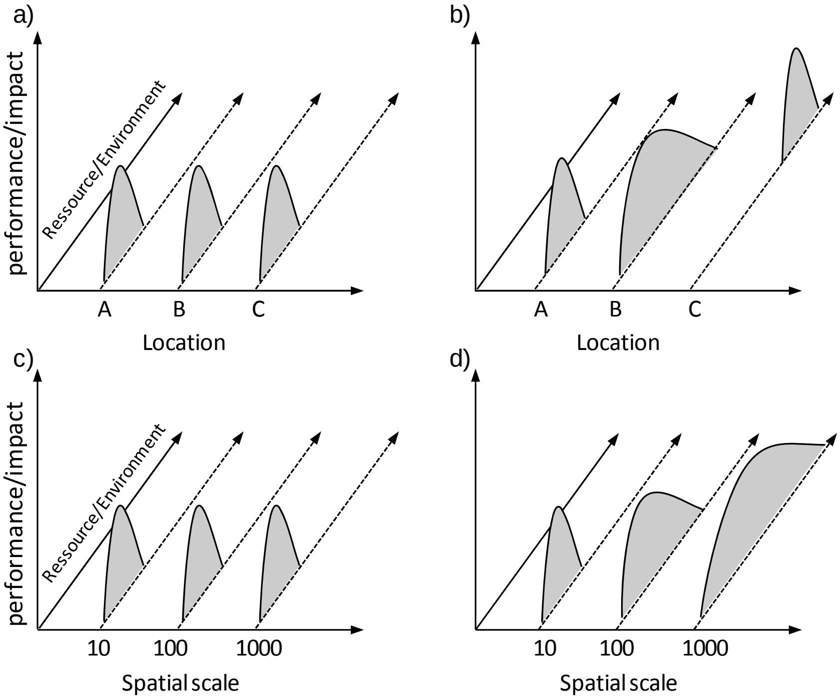

Figure 3. Spatial scaling and specialization
a) Specialization is often considered as an invariant species-property and to be consistent across locations. b) Alternatively, species may have different level of specialization across location. This spatial-dependence of niche breath is induced by true shift in specialization across locations or by variable resource availability. A spatial-dependence can also be observed when the scale at which specialization increases (c&d).

This shift can not only affect niche breath, but also the actual resource, or impact (i.e. the position of the Grinnellian and Eltonian-niche) on which the species is specialized (Harmon et al. 2005; Codron et al. 2008). Similarly, a particular species which appears locally specialized for any ecological factors can be found to be equally specialized at larger spatial scales (Fig. 3c) or not (Fig. 3d). This scale-dependence may be induced because the diversity of resource used by a given species, compiled over its geographical range, is most often higher than the number of resource present and used locally.

From individual to communities

Although specialization was historically developed as a species attribute, any ecological level (individual, population, species, community) can be considered to be more or less specialized (Fig 4).

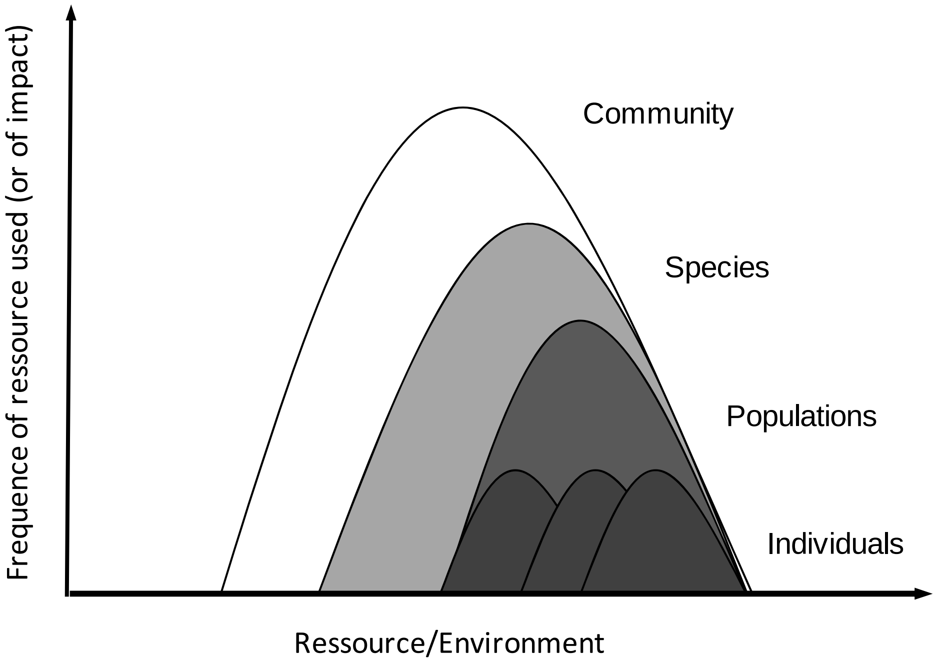

Figure 4. Ecological scaling of specialization from individuals to community. Both Grinnellian and Eltonian-specialization can be defined at any ecological level. A specialized community is the result of more or less specialized species which are themselves the result of more or less specialized populations composed of more or less specialized individuals

For instance, some species that are considered as ecological generalists, are in fact heterogeneous collections of specialized entities of inferior level (Herrera 2005; Bolnick et al. 2007). This within-species variation of ecological specialization (e.g., the specialization of individuals of a given species) has important ecological, evolutionary, and conservation implications (Bolnick et al. 2003, Bogush et al. 2006; Bolnick et al. 2007). For instance, theoretical work on intraspecific competition suggests that different population dynamics can emerge when variation in individual specialization is considered (Bolnick et al. 2003). Moreover, conservation guidelines for a specialist species which are only based on what resource the species is specialized on average, may neglect important more specific resource requirement if individual specialization is not considered.

Full species assemblage can also usefully be characterized by the average Grinnellian-specialization level of the species present in the assemblage (Community Specialization Index, Julliard et al. 2006). This concept of community ecological specialization has been explicitly developed in the context of species interaction networks (Blüthgen et al. 2006). For instance, Eltonian community-wide specialization was used to compare the specialization of different plant-pollinator networks (Devoto et al. 2005), food webs of variable size (Dunne et al. 2002a), coevolutionary adaptations at the community level (Waser et al. 1996) and ecosystem stability or resilience (Dunne et al. 2002b). In these approaches, individuals are considered to be equally specialized and intra-species variation is ignored while between-species specialization is quantified.

Scaling up ecological specialization

Spatial and/or temporal scale-dependence of specialization (either Grinnellian or Eltonian) can be explicitly described. For instance, Silvertown et al. (2006) proposed that, by analogy with the usual partitioning of regional diversity (Whittaker 1975), ecological niche can usefully be partitioned into local scale (at which interactions among species occur, α-niche), regional scale (measured across multiple sites, β-niche) and at the scale of species range (γ-niche).

Similarly, we propose that ecological specialization measured at any scale can be partitioned into local (α_s) and regional (γ_s) components. The local and regional specialization can be further related to each other by the between-scale specialization ($\beta_s = \gamma_s - \alpha_s$) which measure the turnover of resource used by the species across scales (or turnover of impact of the species for Eltonian specialization). Even when not explicitly quantified, acknowledging such scale-dependence of (Grinnellian or Eltonian) specialization allow to distinguish local generalists which, in the meanwhile, appear to be specialist at higher scale because they use many resources within habitats, but have a low turnover of resources among habitats (Hughes et al. 2000).

As for spatial scaling, the total niche breath measured at any ecological level can also be subdivided into a within-level component and a between-level component. In this respect, Roughgarden (1974) has early proposed to view the total niche width of a population (TNW) as the sum of respectively a within and a between individual component (traditionally called WIC and BIC). This approach was successfully used to assess how much variation in a total apparent specialization (TNW) can be explained by variation within or between individuals (i.e., by calculating WIC/TNW) (Bolnick et al. 2002; Sargeant et al. 2007).

This second type of scaling (ecological scaling) should also help to investigate variation in specialization in space and time. For instance, Araújo and Gonzaga (2007) have shown that increased in some individuals specialization of the hunting wasp *Trypoxylon albonigrum* can induced niche breath expansion of the population through time. Although mainly used to study diet specialization and individual-specialization, we suggest that this ecological scaling could be interestingly extended to any type of specialization (Eltonian and Grinnellian) and for any ecological level. For instance, for a given Eltonian-generalist species, one expects to find higher Eltonian-specialized populations if specific interactions between species are selected in these populations.

A tool box for measuring ecological specialization

According to the general definition of ecological specialization (Fig. 1) measuring the breath of the Grinnellian or Eltonian ecological niche necessitate, ideally, to understand i) what environmental conditions individuals can experience (or what is the extent of their impact for Eltonian specialization) and ii) how the performance of individuals (i.e., growth, survival and reproduction) is affected by those environmental conditions (or what is the strength of their impact). Yet, measuring what environmental conditions individuals can experience (or impact) faces two critical problems. First, one needs to select a number of meaningful variables most likely to influence species performance. Second, these variables, along with variation of species performance, must be correctly quantified.

In practice, specialization is most often measured using field data in which abundance or occurrence of individuals is used as a measure of performance (Austin et al. 1990), and in which environmental conditions are roughly and incompletely described. Therefore, although widely-used, quantifying the niche breadth (even along a single gradient), still remains an unresolved scientific issue (Austin et al. 2006). Depending on the question being asked and on the data available, many metrics have thus been proposed to measure ecological specialization at various ecological and spatial scales. We suggest that our conceptual framework can be turned into a practical tool-box which encloses most of these metrics (Grinnellian or Eltonian and fundamental versus realized, Fig. 5).

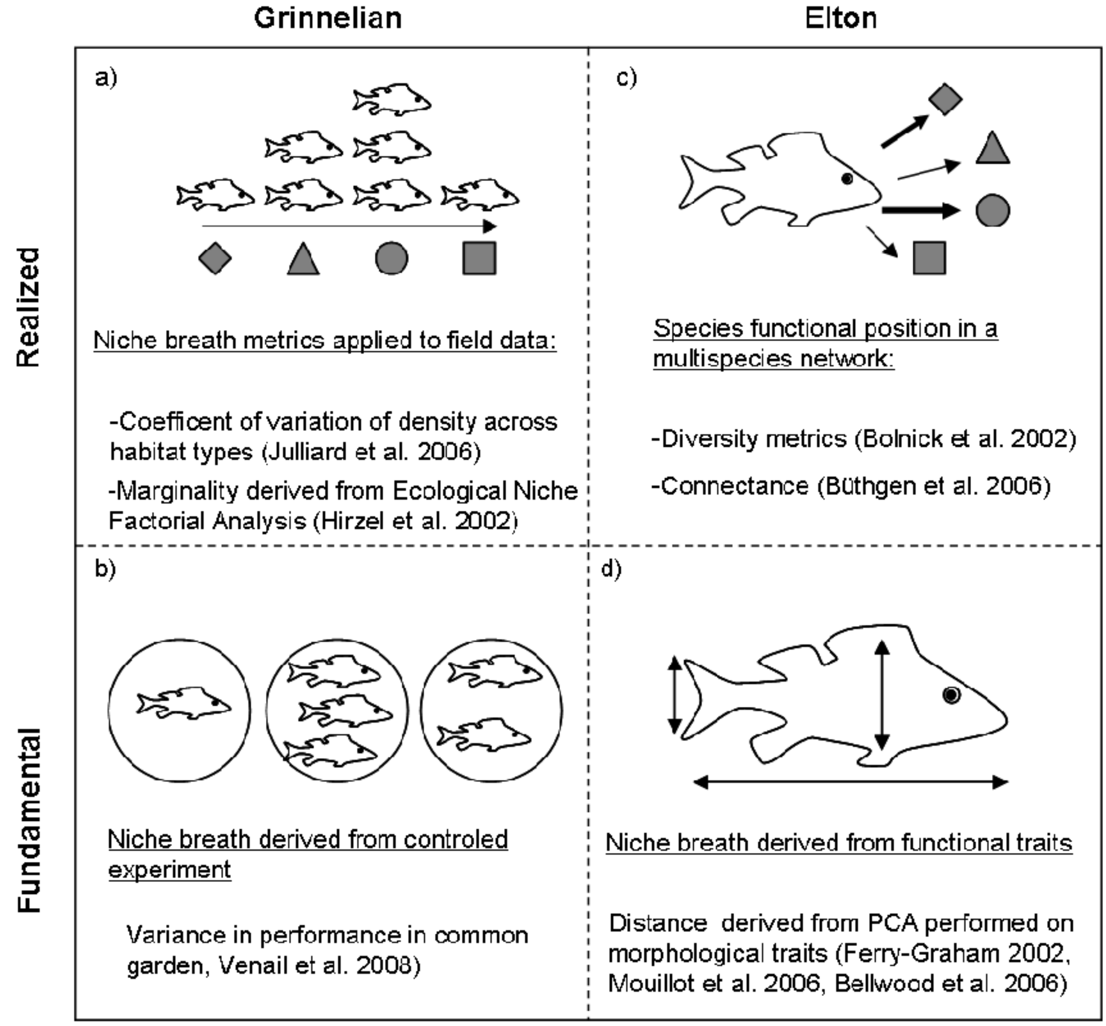

Figure 5. A tool-box for widely used metrics of ecological specialization
Most commonly used metric of specialization can be positioned in this box according to the type of niche considered (Grinnellian versus Eltonian) and whether the fundamental or the realized specialization is measured. The figure represents a fish for which specialization is measured using different metrics. a) the variation in performance along different resource categories (symbolized by geometrical items) using field data will reflect the realized Grinnemmian-specialization; b) measuring variation in performance in controlled experiment (three different conditions are materialized by three circles) will reflect the fundamental Grinnelian-specialization. c) The realized Eltonian-specialization will be quantified using the diversity and strength of impact of the species on others (symbolized by geometrical items). d) Finally, the fundamental Eltonian-specialization would be derived from metrics based on functional traits

Realized-Grinnellian specialization

The realized Grinnellian-specialization (Fig. 5a) is most often quantified using the diversity of resource used by the species in the field, ignoring variation in performance. A specific resource can be explicitly considered (breath of light conditions, food resource) or implicitly enclosed in more integrated discrete categories (e.g. “habitat” classes). For instance, Kommonen et al. (2004) quantify specialization of butterfly using the number of habitat classes where the species occurs. This approach can be easily extended to any variable (e.g., specialization for birds was measured as the product of habitats used and food types consumed by Sekercioglu et al. 2004). Note that such measures of Grinnellian-specialization implicitly focus on species requirement but makes no distinction between strong interactions and weak or occasional ones between the species and its resources. To further account for varying performance of the species across resource or habitat classes, most widely used metrics of realized-Grinnellian specialization have incorporated the species’ abundance (or density), considered as a proxy for performance in traditional diversity indices (e.g., Shannon, Simpson indices, or coefficient of variation). For instance, Julliard et al. (2006) have proposed to measure a species specialization index (SSI) based on the coefficient of variation of the species’ density across habitat classes. These measures of Grinnellian- specialization can also be modified to account for the proportional availability of each resource (Hurlbert 1978, Paitraitis 1979, Feinsinger et al. 1981).

Although these metrics have some advantages (e.g. they are easy to calculate), they are prone to the same sampling biases and pitfalls, long known to complicate estimates of diversity (Magurran, 1988). In particular, specialization can be severely biased by the way resources are classified or weighed, and/or if the range, non-linearity, and spacing of the resource are not appropriately sampled (Colwell and Futuyma 1971). If these problems are not corrected, specialization of species occurring in few samples can be positively biased (rare species tend to be specialized).

More recent realized Grinnellian-specialization metrics were also derived from various species distribution models (reviewed in Austin 2007). The aim of these techniques is to relate the occurrence (or abundance) of species to several environmental variables. As all important environmental variables influencing species distribution are generally not know, not independent from each other, and that specialization is expected to depend on interactions among variables rather than on every variable independently (Hirzel et al. 2002), specialization is calculated from multivariate analysis techniques. The aim of these approaches is to derive specialization from the average habitat conditions used by the species and the conditions available on a given study area (Dolédec et al. 2000). In this case, the realized Grinnellian-specialization, (called “marginality”), mirrors the narrowness of the niche on some environmental variables over a particular area (e.g., Ecological Niche Factor analysis ENFA, Hirzel et al. 2002). Note that although mostly developed for species, these metrics can easily be applied to other scales of biological organization (individuals, populations or communities, see e.g., Calenge 2005; Dolédec et al. 2000). None of these ecological models are flawless and their relevance depends on the data available and the scale considered. Moreover, important conceptual, biotic and algorithmic uncertainties associated with these models still need to be investigated (Guisan and Thuillier 2005, Araújo & Guisan 2006, Austin 2007).

Fundamental-Grinnellian specialization

To measure fundamental-Grinnellian specialization (Fig. 5b), any measure of niche breath can be used as soon as the performance of the species is quantified independently of inter-specific regulation (competition, predation, facilitation) and dispersal constraint. Fundamental-Grinnellian specialization should therefore be derived from controlled experiment in which the performance of the species is measured separately across several resources (e.g., in common garden experiment, Venail et al. 2008) or along a controlled resource gradient (Wright et al. 2006).

Therefore, fundamental Grinnellian specialization is not available at large scale, or from niche modeling (biogeographical barriers and competitors, are generally not integrated in these models) which rather produce an unconstrained geographic projection of the realized niche (Soberon et al. 2007). Yet, using species-specific responses obtained from controlled experiments, or a priori known biotic interactions, to obtain a large scale-distribution of fundamental-Grinnellian niche is subjected to increasing research (Kearney & Porter 2004, Guisan and Thuillier 2005, Morin et al. 2007).

Realized-Eltonian specialization

The realized-Eltonian specialization of a given species (Fig. 5c) is most often measured as the number of partners or 'links' between the focal species and others (e.g. the number of pollinator species visiting a flowering plant) or in more complex connectance metrics (Blüthgen et al. 2006). In this case, the number of interactions between the focal species and others is most often simply counted, ignoring variation in the strength of interactions (Herrera

2005, Blüthgen 2007). As for Grinnellian-specialization, realized-Eltonian specialization is thus more precisely described using diversity metrics including variation in interaction frequency (e.g., Simpson or Shannon diversity index), and accounting for prey availability (Bolnick et al. 2002).

When species impact is investigated using diet analysis, the relative abundance of differing dietary prey items are hardly available because most dietary studies are 'snapshots' of dietary prey at a point in time (Bearhop et al. 2004). Therefore, tracking stable isotopes have become a common alternative to estimate the realized-Eltonian specialization, providing for time- and space-integrated representations of the trophic ecology of organisms (Bearhop et al. 2004; Codron et al. 2008). According to this approach, a more Eltonian-generalist species should interact with a larger breath of species and have more variation in its isotope composition.

Fundamental-Eltonian specialization

Finally, the fundamental-Eltonian specialization (Fig. 5d) must reflect the trophic (or functional) position that a given species is expected to realize without competitors or dispersal limitation. The fundamental-Eltonian specialization of a given species is thus directly reflected by its functional, morphological, and/or behavioural traits. For instance, Bellwood et al. (2006) have proposed to measure the "morphological specialization" of labrid fishes from a PCA performed on morphological traits (e.g., body mass, mouth gape, mandibulae muscle mass). The specialization of a focal species is then defined as its functional distance from the centre of gravity of the set of species (Bellwood et al. 2006; Mouillot et al. 2007). Note that although such a morphological-trait approach can increase our understanding of the ecological concept of specialization and it consequences, measuring functional traits does not tell whether the traits of interest have any relation to an actual performance or advantage (Ferry-Graham et al. 2002). Measuring fundamental Eltonian-specialization is thus generally silent on the realized Eltonian-specialization.

Discussion and futures issues

Limitations

Ecological specialization is one of the most versatile concepts in ecology. Searching for a strict definition of this concept and a unique metric is probably meaningless. Moreover, accepting the multi-dimensional nature of niches means that, by definition, specialization can never be fully quantified (Colwell & Futuyma, 1971). In proposing this framework, our aim was rather to highlight the overlaps between most definitions of ecological specialization and widely-used associated metrics. In doing so, we have proposed to underline the existence of two axes: respectively the axis of Eltonian-specialization versus Grinnellian-specialization and of realized versus fundamental-specialization.

Along these main lines, the concept of specialization and its related metrics could be further declined according to narrower distinctions. For instance, Ferry-Graham (2002) proposed to distinguish functional specialization (driven by morphological constrains) from behavioral specialization (a species whose behavioral repertoire allow to successfully capture specific items from the prey available). Following our framework, these two types of specialization would be classified within Eltonian-specialization (the impact of the species is investigated). Functional specialization is related to fundamental niche whereas behavioral specialization is one of the factor determining realized niche. Similarly, food-resource specialization and habitat-specialization may further be differentiated as two aspect of the Grinnellian-specialization when needed (see e. g., Hughes 2000).

However, we anticipate that disentangling Eltonian (and/or fundamental) from Grinnellian (and/or realized) specialization will not always be straightforward. For instance, modeling species distribution was suggested to be unable to separate the realized and fundamental niche (Araújo & Guisan 2006; Jimenez-Valverde 2008). Besides, large-scale statistical correlations between species records and environmental variables have inconsistently been viewed as the fundamental niche or the realized niche (Kearney 2006). This difficulty to separate Eltonian from Grinnellian specialization is even inherent to certain metric. For instance, Fridley et al. (2007) have recently proposed a parsimonious approach to measure ecological specialization in building a metric based upon the fact that generalists should co-occur with many species, whereas specialists should co-occur with relatively few species. This property can be easily quantified to reflect specialization from species co-occurrence patterns. This metric quantify the Grinnellian-specialization as it reflects the species response (in terms of occurrence) of environmental heterogeneity, which is not explicitly quantified, but rather embodied by the diversity of other co-occuring species. Yet, this measure also implicitly incorporates, somehow, each species impact on each other (occurrence patterns are shaped by biotic interactions), and as such, also indirectly reflects the Eltonian-specialization. More generally, measuring the breath of resource used can alternatively be considered as a measure of Eltonian-specialization (the species impact is quantified) or Grinnellian-specialization (the species requirement is also quantified although the variation in species performance is not explicit). Similarly, measuring functional traits obviously both reflects potential species requirement (i. e. what a species needs to eat) and potential species impact.

To overcome these problems, Eltonian and Grinnellian specialization can be explicitly considered in concert to adopt a more comprehensive view of the niche itself. For instance, Chase and Leibold (2003) proposed a formalism (using a simple model of population dynamics) that integrates both the species' requirements and its impact on the ecosystem. Yet, even if conceptually useful, this extension is difficult to implement in practice because most studies hardly assess species requirement and impact on their environment simultaneously (e.g., correlation between species distribution and environmental variables are often silent on feed-back mechanisms, Araújo & Guisan 2006).

However, beyond these limitations, the distinction between Grinnellian and Eltonian-specialization distinction is useful because most studies generally adopt either the Eltonian or the Grinnellian conception of the niche (Soberon 2007). Therefore, although neither definitive nor flawless, we believe that our conceptual framework is flexible enough to include most conception of specialization, while being enough constrained to be useful. Note that this framework proposes a renewal of the traditional assumption underlying the measurement of the ecological niche, which classifies specialization and its metrics using process-driven criteria (impact versus requirement and fundamental versus realized) rather than data-driven criteria (biotic versus abiotic variables, large versus local-scale…). We thus also believe that this approach allow to highlight original future research directions.

Future research directions

Our proposed framework should be useful to study the causes and consequences of the so-called *niche-conservatism debate*. The niche conservatism hypothesis is built upon the expectation that the fundamental niche should be conserved over long evolutionary time scales so that species tend to retain ancestral ecological characteristics (Wiens and Graham, 2005). In general, a smaller degree of conservatism is found in niche breath (generally reflecting

Grinnellian-specialization) than in many morphological and physiological traits (Entling et al. 2007). Investigating niche conservatism in testing whether the Grinnellian-specialization is evolving faster than Eltonian-specialization should thus be helpful to clarify this debate.

Testing similar predictions on Grinnellian versus Eltonian-specialists should also help to investigate the so-called *biotic homogenization process*. According to this process, Human-induced environmental and climate changes are suspected to act as non-random filters, selecting species best able to survive within modified ecosystems (McKinney and Lockwood 1999). Despite the increasing use of the term biotic homogenization in conservation biology and theoretical ecology, practical means to measure this process are still largely missing and underlying ecological mechanisms involved still unclear (Olden 2006). While growing evidence suggests that Grinnellian-generalists tend to replace Grinnellian-specialists (Devictor et al. 2007), whether this process is also occurring for Eltonian-specialists has hardly been investigated (But see Smart et al. 2006). Moreover, whether and how the loss in Grinnellian-specialists is coupled with the loss in Eltonian-specialists has hardly been tested. This issue is a matter of considerable conservation interest as the loss of specific function (Eltonian-specialists) can eventually lead to the loss of ecological services with important consequences at the ecosystem level (Loreau et al 2001).

For a given type of specialization, making explicit distinction between fundamental and realized specialization should further help to investigate species response to biotic and abiotic perturbations. For instance, the same food may be eaten by two different species (similar realized Eltonian-specialization), but the nutritional outcome may vary if they have different digestive systems (different fundamental Eltonian-specialization). Moreover, while we might predict to find negative impacts of disturbance on a given fundamental Grinnellian-specialist, the realized Grinnellian-specialization of this species might solely change if the biotic-interactions and dispersal constraints are redefined within the new environment. In other words, acknowledging the difference between realized and fundamental specialization should help to test under what circumstance a realized (versus fundamental) Grinnellian (or Eltonian)-specialist can become realized (versus fundamental) Grinnellian (or Eltonian)-generalist. This distinction should be very important to prioritize conservation targets (e.g., to anticipate a change in protected or invasive species dynamics).

Finally, the consequences of scale-dependence of realized versus fundamental specialization remain poorly understood (McEachern et al. 2006) so that species are most often considered to be equally specialized across spatial scales. For instance, macroecological theory predicts that fundamental Grinnellian-generalists should have the largest geographical range (the so-called Brown hypothesis, Brown 1994). Yet, for a given fundamental Grinnellian specialization level, geographically rare, and therefore extinction-prone species, are more likely to persist if they are locally realized-Grinnellian generalists (Williams et al. 2006). Recognizing that niche breath is both shaped by functional and life-history traits (fundamental specialization) and by biotic and abiotc constraints (realized-specialization) should help to shed light on local versus large-scale processes driving species distribution (Lavergne et al. 2004; Morin & Chuine 2006) and the reframing of theoretical predictions.

Conclusion

Root (1967) have early pointed that “the niche concept is one of the most confusing, and yet important topics in ecology”. The concept of specialization, which is nothing else than a particular facet of the niche, provides a good illustration of this remark. Specialization is an intuitive and operational concept which is both highly needed in theoretical and applied ecology, and in the meanwhile, highly dependent on the particular study.

In recognizing the link between specialization and seminal distinction underlying the niche concept (Grinnellian/Eltonian and Realized/Fundamental), our proposed framework should provide a better integration of different aspects of ecological specialization and facilitate comparison across studies.

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Glossaire

Actinoptérygiens : Poissons à nageoires rayonnées

Biodiversité : Diversité biologique des écosystèmes, de l'échelle des gènes à celle des paysages, mesurée par la richesse, la variabilité, la régularité et les interactions entre les éléments

Changements globaux : Modifications physiques, chimiques et biologiques d'origines anthropiques affectant tous les écosystèmes

Chondrichtyens : Poissons à squelette cartilagineux regroupant les chimères, les requins et les raies

Communauté : Ensemble d'‘individus et d'espèces pouvant potentiellement interagir

Diversité fonctionnelle : Composante de la biodiversité correspondant à la distribution des traits fonctionnels et de leurs abondances associées. Elle comprend trois facettes : la richesse, la régularité et la divergence

Écosystème : Système écologique dans lequel interagissent le biotope (ensemble des habitats) et la biocénose (ensemble des êtres vivants)

Écosystèmes estuariens et lagunaires : Écosystèmes côtiers à l'interface entre les influences terrestres et marines. Ils sont caractérisés par une forte variabilité des conditions environnementales

Filtre environnemental : Variable abiotique déterminant le succès d'installation d'une d'espèce

Fitness : valeur sélective d'un individu, mesurée comme le nombre de descendants arrivant à se reproduire

Fonctionnement des écosystèmes : flux influencés pour tout ou partie par les organismes vivants

Métacommunauté : Ensemble de communautés reliées entre elles par la dispersion

Necton : Ensemble des organismes vivants capables de se déplacer activement dans la colonne d’eau

Niche écologique : Au sens de Grinnell, ensemble des conditions abiotiques et biotiques nécessaires à la survie d’une espèce. Selon Elton, impact d’une espèce sur son écosystème

Niche fonctionnelle : Stratégie d’une espèce décrite par ses traits fonctionnels

Poissons : Vertébrés aquatiques respirant au moyen de branchies et ayant des nageoires. Clade paraphylétique regroupant les agnathes, les chondrichtyens et les téléostéens

Services écosystémiques : Biens matériels et immatériels fournit par les écosystèmes aux populations humaines

Stabilité des écosystèmes : Résistance et résilience d’un écosystème face à une perturbation

Téléostéens : Poissons ayant un squelette osseux. Ce clade paraphylétique regroupe les actinoptérygiens et les sarcoptérygiens

Théorie unifiée neutre : Paradigme écologique proposé par Hubbell selon lequel les espèces ne diffèrent significativement pas entre elles d’un point de vue sélectif. Leurs répartitions sont donc dictées par des processus stochastiques liés à leur dispersion et à leur survie

Trait : Variable biologique mesurable à l’échelle individuelle

Trait fonctionnel : Trait ayant un impact sur la fitness d’un individu. Les traits fonctionnels de réponse décrivent la réponse des individus à leur environnement. Les traits fonctionnels d’effet désignent les traits ayant un impact sur le fonctionnement des écosystèmes

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ANNEXES

Annexe A. Liste des espèces de poissons présentes dans les bases de données

Annexe B. Photos des espèces sur lesquelles les traits morpho-anatomiques ont été mesurés

Annexe C. Invertébrés nectoniques pris en compte dans l'analyse de la structure trophique

Annexe A. Liste des espèces de poissons présentes dans les bases de données

Espèce		Ordre	Famille	Code
Acanthostracion quadricornis	Linnaeus 1758	Tetraodontiformes	Ostraciidae	ACANQUAD
Achirus lineatus	Linnaeus 1758	Pleuronectiformes	Achiridae	ACHILINE
Aluterus schoepfii	Walbaum 1792	Tetraodontiformes	Monacanthidae	
Aluterus scriptus	Osbeck 1765	Tetraodontiformes	Monacanthidae	
Anchoa hepsetus	Linnaeus 1758	Clupeiformes	Engraulidae	ANCHHEPS
Anchoa lamprotaenia	Hildebrand 1943	Clupeiformes	Engraulidae	
Anchoa mitchilli	Valenciennes 1848	Clupeiformes	Engraulidae	ANCHMITC
Ancylopsetta ommata	Jordan & Gilbert 1883	Pleuronectiformes	Paralichthyidae	
Anisotremus virginicus	Linnaeus 1758	Perciformes	Haemulidae	
Archosargus probatocephalus	Walbaum 1792	Perciformes	Sparidae	ARCHPROB
Archosargus rhomboidalis	Linnaeus 1758	Perciformes	Sparidae	ARCHRHOM
Ariopsis felis	Linnaeus 1766	Siluriformes	Ariidae	ARIOFELI
Bagre marinus	Mitchill 1815	Siluriformes	Ariidae	BAGRMARI
Bairdiella chrysoura	Lacepède 1802	Perciformes	Sciaenidae	BAIRCHRY
Bairdiella ronchus	Cuvier 1830	Perciformes	Sciaenidae	BAIRRONC
Balistes capriscus	Gmelin 1789	Tetraodontiformes	Balistidae	
Bathygobius soporator	Valenciennes 1837	Perciformes	Gobiidae	
Bothus ocellatus	Agassiz 1831	Pleuronectiformes	Bothidae	
Bothus robinsi	Topp & Hoff 1972	Pleuronectiformes	Bothidae	
Calamus penna	Valenciennes 1830	Perciformes	Sparidae	
Caranx crysos	Mitchill 1815	Perciformes	Carangidae	
Caranx hippos	Linnaeus 1766	Perciformes	Carangidae	CARAHIPP
Caranx latus	Agassiz 1831	Perciformes	Carangidae	CARALATU
Cathorops melanopus	Günther 1864	Siluriformes	Ariidae	CATHMELA
Centropomus parallelus	Poey 1860	Perciformes	Centropomidae	CENTPARA
Centropomus poeyi	Chávez 1961	Perciformes	Centropomidae	
Centropomus undecimalis	Bloch 1792	Perciformes	Centropomidae	CENTUNDE

Annexe A. Liste des espèces de poissons présentes dans les bases de données

Espèce		Ordre	Famille	Code
Cetengraulis edentulus	Cuvier 1829	Clupeiformes	Engraulidae	CETEEDEN
Chaetodipterus faber	Broussonet 1782	Perciformes	Ephippidae	CHAEFABE
Chilomycterus schoepfii	Walbaum 1792	Tetraodontiformes	Diodontidae	CHILSCHO
Chloroscombrus chrysurus	Linnaeus 1766	Perciformes	Carangidae	CHLOCHRY
Chriodorus atherinoides	Goode & Bean 1882	Beloniformes	Hemiramphidae	
Cichlasoma urophthalmus	Günther 1862	Perciformes	Cichlidae	
Citharichthys spilopterus	Günther 1862	Pleuronectiformes	Paralichthyidae	CITHSPIL
Conodon nobilis	Linnaeus 1758	Perciformes	Haemulidae	CONONOBI
Cyclopsetta chittendeni	Bean 1895	Pleuronectiformes	Paralichthyidae	
Cynoscion arenarius	Ginsburg 1930	Perciformes	Sciaenidae	CYNOAREN
Cynoscion nebulosus	Cuvier 1830	Perciformes	Sciaenidae	CYNONEBU
Cynoscion nothus	Holbrook 1848	Perciformes	Sciaenidae	CYNONOTH
Dasyatis americana	Hildebrand & Schroeder 1928	Myliobattiformes	Dasyatidae	DASYAMER
Dasyatis hastata	DeKay 1842	Myliobattiformes	Dasyatidae	
Dasyatis sabina	Lesueur 1824	Myliobattiformes	Dasyatidae	DASYSABI
Diapterus auratus	Ranzani 1842	Perciformes	Gerridae	DIAPAURA
Diapterus rhombeus	Cuvier 1829	Perciformes	Gerridae	DIAPRHOM
Diplectrum formosum	Linnaeus 1766	Perciformes	Serranidae	
Diplectrum radiale	Quoy & Gaimard 1824	Perciformes	Serranidae	
Dorosoma anale	Meek 1904	Clupeiformes	Clupeidae	DOROANAL
Dorosoma petenense	Günther 1867	Clupeiformes	Clupeidae	DOROPETE
Echiophis punctifer	Kaup 1860	Anguilliformes	Ophichthidae	
Elops saurus	Linnaeus 1766	Elopiformes	Elopidae	
Epinephelus itajara	Lichtenstein 1822	Perciformes	Serranidae	
Etropus crossotus	Jordan & Gilbert 1882	Pleuronectiformes	Paralichthyidae	ETROCROS
Eucinostomus argenteus	Baird & Girard 1855	Perciformes	Gerridae	EUCIARGE
Eucinostomus gula	Quoy & Gaimard 1824	Perciformes	Gerridae	EUCIGULA

Annexe A. Liste des espèces de poissons présentes dans les bases de données

Espèce		Ordre	Famille	Code
Eucinostomus melanopterus	Bleeker 1863	Perciformes	Gerridae	EUCIMELA
Eugerres plumieri	Cuvier 1830	Perciformes	Gerridae	EUGEPLUM
Gobionellus oceanicus	Pallas 1770	Perciformes	Gobiidae	GOBIOCEA
Gobiosoma bosc	Lacepède 1800	Perciformes	Gobiidae	
Gymnachirus texae	Gunter 1936	Pleuronectiformes	Achiridae	
Gymnothorax nigromarginatus	Girard 1858	Anguilliformes	Muraenidae	
Gymnura micrura	Bloch & Scneider 1801	Myliobattiformes	Gymnuridae	GYMNMICR
Haemulon aurolineatum	Cuvier 1830	Perciformes	Haemulidae	
Haemulon bonariense	Cuvier 1830	Perciformes	Haemulidae	HAEMBONA
Haemulon plumierii	Lacepède 1801	Perciformes	Haemulidae	
Harengula jaguana	Poey 1865	Clupeiformes	Clupeidae	HAREJAGU
Hemicaranx amblyrhynchus	Cuvier 1833	Perciformes	Carangidae	HEMIAMBL
Himantura schmardae	Werner 1904	Myliobattiformes	Dasyatidae	
Hippocampus erectus	Perry 1810	Gasterosteiformes	Syngnathidae	
Lagocephalus laevigatus	Linnaeus 1766	Tetraodontiformes	Tetradontidae	
Lagodon rhomboides	Linnaeus 1766	Perciformes	Sparidae	
Larimus fasciatus	Holbrook 1855	Perciformes	Sciaenidae	
Lepophidium brevibarbe	Cuvier 1829	Ophidiiformes	Ophidiidae	
Lobotes surinamensis	Bloch 1790	Perciformes	Lobotidae	LOBOSURI
Lutjanus analis	Cuvier 1828	Perciformes	Lutjanidae	
Lutjanus apodus	Walbaum 1792	Perciformes	Lutjanidae	
Lutjanus griseus	Linnaeus 1758	Perciformes	Lutjanidae	LUTJGRIS
Lutjanus synagris	Linnaeus 1758	Perciformes	Lutjanidae	LUTJSYNA
Menticirrhus americanus	Linnaeus 1758	Perciformes	Sciaenidae	MENTAMER
Menticirrhus saxatilis	Bloch & Schneider 1801	Perciformes	Sciaenidae	MENTSAXA
Micropogonias undulatus	Linnaeus 1766	Perciformes	Sciaenidae	MICRUNDU
Monacanthus ciliatus	Mitchill 1818	Tetraodontiformes	Monacanthidae	

Annexe A. Liste des espèces de poissons présentes dans les bases de données

Espèce		Ordre	Famille	Code
Mugil cephalus	Linnaeus 1758	Mugiliformes	Mugilidae	
Mugil curema	Valenciennes 1836	Mugiliformes	Mugilidae	
Mycteroperca bonaci	Poey 1860	Perciformes	Serranidae	
Narcine brasiliensis	Olfers 1831	Torpediniformes	Narcinidae	
Nicholsina usta	Valenciennes 1840	Perciformes	Scaridae	
Ocyurus chrysurus	Bloch 1791	Perciformes	Lutjanidae	
Odontoscion dentex	Cuvier 1830	Perciformes	Sciaenidae	
Oligoplites saurus	Bloch & Schneider 1801	Perciformes	Carangidae	OLIGSAUR
Ophichthus gomesii	Castelnau 1855	Anguilliformes	Ophichthidae	
Opisthonema oglinum	Lesueur 1818	Clupeiformes	Clupeidae	
Opsanus beta	Goode & Bean 1880	Batrachoidiformes	Batrachoididae	OPSABETA
Orthopristis chrysoptera	Linnaeus 1766	Perciformes	Haemulidae	ORTHCHRY
Pareques acuminatus	Bloch & Schneider 1801	Perciformes	Sciaenidae	
Peprilus paru	Linnaeus 1758	Perciformes	Stomateidae	PEPRPARU
Polydactylus octonemus	Girard 1858	Perciformes	Polynemidae	POLYOCTO
Porichthys porosissimus	Cuvier 1829	Batrachoidiformes	Batrachoididae	PORIPORO
Prionotus beanii	Goode 1896	Perciformes	Triglidae	
Prionotus carolinus	Linnaeus 1771	Perciformes	Triglidae	PRIOCARO
Prionotus punctatus	Bloch 1793	Perciformes	Triglidae	PRIOPUNC
Prionotus scitulus	Jordan & Gilbert 1882	Perciformes	Triglidae	PRIOSCIT
Prionotus tribulus	Cuvier 1829	Perciformes	Triglidae	PRIOTRIB
Rhinobatos lentiginosus	Garman 1880	Rajiformes	Rhinobatidae	RHINLENT
Rhinoptera bonasus	Mitchill 1815	Myliobattiformes	Myliobatidae	RHINBONA
Sardinella janeiro	Eigenmann 1894	Clupeiformes	Clupeidae	
Scomberomorus maculatus	Mitchill 1815	Perciformes	Scombridae	
Scorpaena plumieri	Bloch 1789	Scorpaeniformes	Scorpaenidae	
Selene setapinnis	Mitchill 1815	Perciformes	Carangidae	SELESETA

Annexe A. Liste des espèces de poissons présentes dans les bases de données

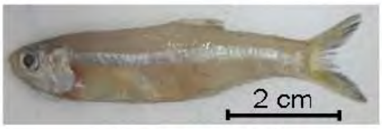
Espèce		Ordre	Famille	Code
Selene vomer	Linnaeus 1758	Perciformes	Carangidae	SELEVOME
Sphoeroides greeleyi	Gilbert 1900	Tetraodontiformes	Tetradontidae	
Sphoeroides marmoratus	Lowe 1838	Tetraodontiformes	Tetradontidae	
Sphoeroides nephelus	Goode & Bean 1882	Tetraodontiformes	Tetradontidae	SPHONEPH
Sphoeroides pachygaster	Müller & Troschel 1848	Tetraodontiformes	Tetradontidae	SPHOPACH
Sphoeroides parvus	Shipp & Yerger 1969	Tetraodontiformes	Tetradontidae	SPHOPARV
Sphoeroides spengleri	Bloch 1785	Tetraodontiformes	Tetradontidae	
Sphoeroides testudineus	Linnaeus 1758	Tetraodontiformes	Tetradontidae	SPHOTEST
Sphyraena guachancho	Cuvier 1829	Perciformes	Sphyraenidae	
Stellifer lanceolatus	Holbrook 1855	Perciformes	Sciaenidae	STELLANC
Stephanolepsis hispidus	Linnaeus 1766	Tetraodontiformes	Monacanthidae	
Strongylura notata	Poey 1860	Beloniformes	Belonidae	
Syacium gunteri	Ginsburg 1933	Pleuronectiformes	Paralichthyidae	
Syacium papillosum	Linnaeus 1758	Pleuronectiformes	Paralichthyidae	
Symphurus plagiusa	Bloch & Schneider 1801	Pleuronectiformes	Cynoglossidae	SYMPPLAG
Syngnathus louisianae	Günther 1870	Gasterosteiformes	Syngnathidae	
Syngnathus pelagicus	Linnaeus 1758	Gasterosteiformes	Syngnathidae	
Syngnathus scovelli	Evermann & Kendall 1896	Gasterosteiformes	Syngnathidae	
Synodus foetens	Linnaeus 1766	Aulopiformes	Synodontidae	SYNOFOET
Trachinotus carolinus	Linnaeus 1766	Perciformes	Carangidae	TRACCARO
Trachinotus falcatus	Linnaeus 1758	Perciformes	Carangidae	TRACFALC
Trachinotus goodei	Jordan & Evermann 1896	Perciformes	Carangidae	
Trichiurus lepturus	Linnaeus 1758	Perciformes	Trachiuridae	TRICLEPT
Trinectes maculatus	Bloch & Scneider 1801	Pleuronectiformes	Achiridae	TRINMACU
Urobatis jamaicensis	Cuvier 1816	Myliobattiformes	Urolophidae	UROBJAMA

Annexe B. Photos des espèces sur lesquelles les traits morpho-anatomiques ont été mesurés

Acanthostracion quadricornis

Achirus lineatus

Anchoa hepsetus



Anchoa mitchilli

Archosargus probatocephalus

Archosargus rhomboidalis

Ariopsis felis

Bagre marinus

Bairdiella chrysoura

Bairdiella ronchus

Caranx hippos

Caranx latus

Cathorops melanopus

Centropomus parallelus

Centropomus undecimalis

Cetengraulis edentulus

Chaetodipterus faber

Chilomycterus schoepfii

Annexe B. Photos des espèces sur lesquelles les traits morpho-anatomiques ont été mesurés

Chloroscombrus chrysurus

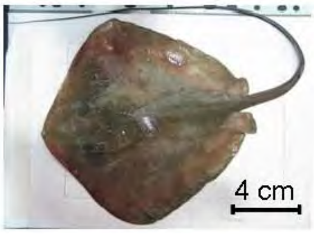
Citharichthys spilopterus

Conodon nobilis

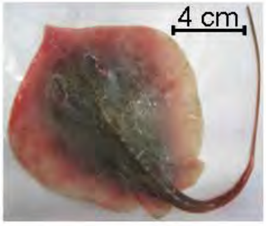
Cynoscion arenarius

Cynoscion nebulosus

Cynoscion nothus

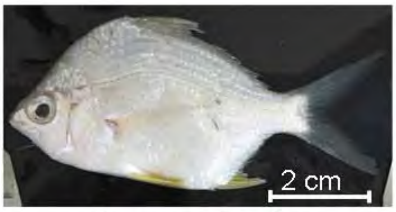


Dasyatis americana

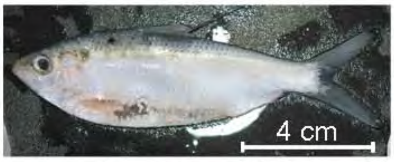


Dasyatis sabina

Diapterus auratus



Diapterus rhombeus



Dorosoma anale

Dorosoma petenense

Etropus crossotus

Eucinostomus argenteus

Eucinostomus gula

Eucinostomus melanopterus

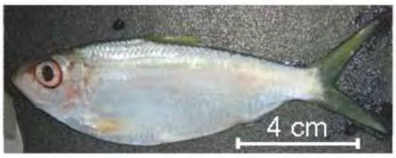
Eugerres plumieri

Gobionellus oceanicus

Annexe B. Photos des espèces sur lesquelles les traits morpho-anatomiques ont été mesurés

Gymnura micrura

Haemulon bonariense



Harengula jaguana

Hemicaranx amblyrhynchus

Lobotes surinamensis

Lutjanus griseus

Lutjanus synagris

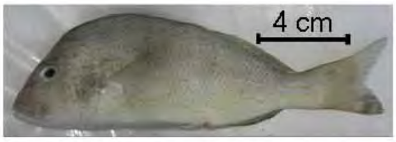
Menticirrhus americanus

Menticirrhus saxatilis

Micropogonias undulatus

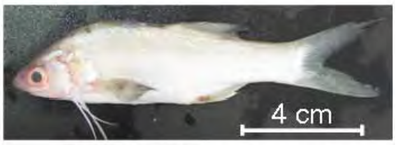
Oligoplites saurus

Opsanus beta



Othopristis chrysoptera

Peprilus paru



Polydactylus octonemus

Porichthys porosissimus

Prionotus carolinus

Prionotus punctatus

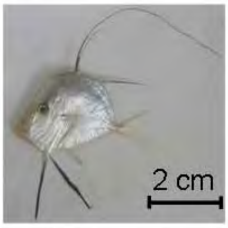
Annexe B. Photos des espèces sur lesquelles les traits morpho-anatomiques ont été mesurés

Prionotus scitulus

Prionotus tribulus

Rhinobatos lentiginosus

Selene setapinnis



Selene vomer

Sphoeroides nephelus

Sphoeroides pachygaster

Sphoeroides parvus

Sphoeroides testudineus

Stellifer lanceolatus

Symphurus plagiusa

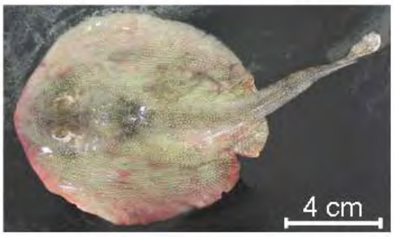
Synodus foetens

Trachinotus carolinus

Trachinotus falcatus

Trichiurus lepturus

Trinectes maculatus



Urobatis jamaicensis

Annexe C. Invertébrés nectoniques pris en compte dans l'analyse de la structure trophique

Espèce		Ordre	Famille
Lolliguncula brevis	Blainville 1823	Teuthida	Loliginidae
Callinectes bocourti	Milne-Edwards 1879	Decapoda	Portunidae
Callinectes rathbunae	Contreras 1930	Decapoda	Portunidae
Callinectes sapidus	Rathbun 1896	Decapoda	Portunidae
Callinectes similis	Williams 1966	Decapoda	Portunidae
Farfantepenaeus aztecus	Ives 1891	Decapoda	Penaeidae
Farfantepenaeus duorarum	Burkenroad 1939	Decapoda	Penaeidae
Litopenaeus setiferus	Linnaeus 1767	Decapoda	Penaeidae
Xiphopenaeus kroyeri	Heller 1862	Decapoda	Penaeidae
Rimapenaeus similis	Smith 1885	Decapoda	Penaeidae
Sicyona brevirostris	Stimpson 1871	Decapoda	Sicyoniidae
Squilla empusa	Say 1818	Stomatopoda	Squillidae

RÉSUMÉ

Un des enjeux majeurs de l'écologie est de comprendre comment les changements globaux affectent la biodiversité et quelles en sont les conséquences sur le fonctionnement des écosystèmes. Dans cette perspective, la diversité fonctionnelle des communautés est un outil clé permettant de lier l'environnement, la structure des communautés et les propriétés écosystémiques. L'objectif de cette thèse est donc d'améliorer la compréhension de la dynamique de la diversité fonctionnelle (i) face à des conditions environnementales naturellement variables et (ii) face à des perturbations d'origine anthropique.

Dans un premier temps nous avons mis en place un socle méthodologie nous permettant de (1) définir la niche fonctionnelle des poissons à partir de traits fonctionnels et (2) de quantifier les diversités fonctionnelles intra (α) et inter (β) échantillons avec de nouveaux indices. Dans un second temps nous avons étudié la dynamique spatio-temporelle de la structure fonctionnelle des communautés ichtyologiques et nectoniques peuplant la lagune de Terminos (Mexique). Cet écosystème estuarien tropical est un modèle d'étude adapté à notre problématique car il présente une forte variabilité environnementale, une forte diversité biologique et est sous forte pression anthropique.

Nous avons mis en évidence une stabilité de la structure fonctionnelle et trophique des communautés face aux gradients environnementaux très marqués, et donc malgré un fort taux de remplacement des espèces entre les communautés. Cette stabilité est due à la dominance de quelques groupes fonctionnels à l'intérieur desquels les espèces se remplacent suivant leurs preferendums environnementaux. Néanmoins, à plus long terme, nous avons démontré qu'une portion de la lagune avait subi une perte de diversité fonctionnelle et ce malgré une augmentation de la richesse spécifique. Ce paradoxe est à relier au remplacement des espèces inféodées aux herbiers de phanérogames par des espèces plus estuariennes.

MOTS CLÉS : traits fonctionnels, indices de diversité fonctionnelle, écosystème estuarien, gradient environnemental, changements globaux, téléostéens, necton, Golfe du Mexique

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