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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Accounting for intraspecific diversity when examining relationships between non-native species and functional diversity

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Abstract

Quantifying changes in functional diversity, the facet of biodiversity accounting for the biological features of organisms, has been advocated as one of the most integrative ways to unravel how communities are affected by human-induced perturbations. The present study assessed how functional diversity patterns varied among communities that differed in the degree to which non-native species dominated the community in temperate lake fish communities and whether accounting for intraspecific functional variability could provide a better understanding of the variation of functional diversity across communities. Four functional diversity indices were computed for 18 temperate lake fish communities along a gradient of non-native fish dominance using morphological functional traits assessed for each life-stage within each species. First, we showed that intraspecific variability in functional traits was high and comparable to interspecific variability. Second, we found that non-native fish were functionally distinct from native fish. Finally, we demonstrated that there was a significant relationship between functional diversity and the degree to which non-native fish currently dominated the community and that this association could be better detected when accounting for intraspecific functional variability. These findings highlighted the importance of incorporating intraspecific variability to better quantify the variation of functional diversity patterns in communities facing human-induced perturbations.

Keywords Non-native species · Functional traits · Intraspecific variability · Functional diversity · Community assembly

Introduction

Biological invasions are considered as one of the main drivers altering natural ecosystems sparking the concerns of scientists and wildlife managers over the past few decades (Simberloff et al. 2013). To understand the relationships between the presence of non-native species and metrics of biodiversity, most studies have primarily focused on the taxonomic structure of recipient communities. These studies have demonstrated that the invasion success of non-native species results from local environmental conditions and biotic interactions (e.g. competition, predation, parasitism) with native organisms and that, once non-native species become abundant, they can impact native organisms, potentially leading to local extirpation (Vitousek et al. 1996; Tilman 1997; Wilcove et al. 1998; Stohlgren et al. 1999; Didham et al. 2005). While our understanding of the temporal dynamic of the interactions between non-native species and native biota is limited (Závorka et al. 2018), changes in the taxonomic structure of recipient communities occurring during biological invasions have been reported to have subsequent cascading effects on the functioning of recipient ecosystems (Hooper et al. 2005; Anderson and Rosemond 2007; Hooper et al. 2012).

Taxonomic approaches lack, however, much information about biological diversity (Gaston 1996). Equating distinct ecological roles to different species is indeed not appropriate as it is the functional characteristics of a species (i.e., traits which influence the fitness of organisms and their effects on

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ecosystem functioning; Violle et al. 2007; Díaz et al. 2013) rather than its taxonomic identity that drive species filtering, competitive interactions and its ecological role in communities (Kraft et al. 2008; Adler et al. 2013; Kraft et al. 2015). Quantifying the functional structure of communities is, therefore, a more integrative approach than those based on taxonomic attributes, notably to determine the association between human-induced perturbations (e.g., the establishment of non-native species; Mouillot et al. 2013) and biological diversity. The use of functional approaches by ecologists has been continuously growing for the past decade. Differences in functional traits between native and non-native species, measured as functional overlap, can be used to identify the most at risk native species in terms of potential competitive exclusion by non-native species if functional redundancy is observed (Elleouet et al. 2014). In plants, it has been demonstrated that non-native species usually display higher leaf area (Ordonez et al. 2010) and biomass of roots (van Kleunen et al. 2010) and lower mean C:N ratio (Heard and Sax 2013) than native species, providing them with competitive advantages. Studies that explored the functional differences between native and non-native animal species were based on single functional trait comparison (e.g., body size: Blanchet et al. 2010; trophic position: Cucherousset et al. 2012). To date, empirical assessments of the differences in functional attributes between native and non-native animal species are still lacking (but see Azzurro et al. 2014; Elleouet et al. 2014; Villéger, Grenouillet and Brosse 2014). Humans are constantly altering the habitat template of environments, creating niche opportunities for some non-native species that are particularly well adapted for the consistent ways that ecosystems are altered (e.g., stabilizing flow regimes, simplifying forest structure, urbanizing landscapes; Olden et al. 2006; Pool et al. 2010), which could result in changes in functional diversity patterns. For instance, using a multiple life-history traits approach, Olden et al. (2006) demonstrated that non-native fish species displayed specific life-history strategies with no or minimal overlap with native species and hence altered functional diversity.

Intraspecific trait variability (Violle et al. 2012) is a key ecological concept with an ecological role comparable to the role of interspecific diversity (Des Roches et al. 2018; Raffard et al. 2018). This key facet of biological diversity has, however, jointly been neglected by functional (Laforest-Lapointe et al. 2014) and invasive (Juette et al. 2014) ecologists. Intraspecific variability in functional traits could be high in plants (Jung et al. 2010; Albert et al. 2012) and animals (Rudolf and Rasmussen 2013a; Zhao et al. 2014) and individuals within species can represent functionally distinct groups, potentially modifying functional diversity patterns (Cianciaruso et al. 2009; de Bello et al. 2011). Intraspecific trait variability is also positively correlated with the establishment success of non-native species (Mitchell and Bakker 2014; González-Suárez et al. 2015). This is especially true for morphological-based functional traits, as variation in these traits is correlated with the ability of species to establish and spread in novel environments (Richards et al. 2006; Davidson et al. 2011). For instance, high intraspecific variation in body size provides non-native species with the opportunity to forage on a broader range of prey sizes (González-Suárez et al. 2015). Such variability is functionally important because intraspecific variability in the diet of non-native species can subsequently modulate their ecological impacts on recipient ecosystems (Evangelista et al. 2017). Quantifying the importance of phenotypic variability in non-native species is, therefore, crucial.

Although the need to account for intraspecific variability in functional and invasion ecology has been advocated at many instances (Bolnick et al. 2011; Violle et al. 2012; Rudolf et al. 2014), it is still not commonly assessed in animal communities despite the fact that it could be as important as interspecific difference for explaining co-occurrence rules and biodiversity patterns (Violle et al. 2012). Previous studies have demonstrated that different life-stages within a species can have different biological attributes (Zhao et al. 2014) and act as sequential specialists (Rudolf and Lafferty 2011) having different functional roles in communities and ecosystems (Rudolf and Rasmussen 2013b). Measuring functional diversity requires measuring trait values for functional entities that could simply be species, i.e., average specific trait values are used to compute indices (Villéger et al. 2008). Incorporating intraspecific trait variability in functional diversity assessment could be done through accounting for several functional entities within each species, e.g. life-stages for species with marked ontogenetic shifts (Rudolf and Van Allen 2017).

Here, we used temperate fish communities as model systems for studying the patterns of functional diversity in lakes with contrasted levels of non-native species dominance using a multi-trait approach incorporating intraspecific variability (i.e., functional traits quantified for the different life-stages within each species). More specifically, we (1) assessed the importance of intraspecific functional variability in animal communities, (2) quantified the functional differences between native and non-native fish, (3) measured how functional diversity co-varies with the degree to which non-native fish currently dominate an assemblage and (4) determined whether accounting for intraspecific functional variability could provide a better description of the variation of functional diversity patterns.

Materials and methods

Study sites and fish communities

Eighteen artificial lakes (gravel pits) located in the river Garonne floodplain (southwest of Toulouse, France) were selected as study sites for the present study. These lakes were dredged between 1964 and 2007 (end-year of dredging), were located within a 22-km radius and disconnected from the river network. Although some variability is observed in the temporal dynamic of fish communities between lakes, a general pattern was observed (Zhao et al. 2016). The first species observed in these artificial lakes was usually native European perch (*Perca fluviatilis*) that usually occurred in the lake during the dredging process. The colonization process of this species in the gravel pit lakes remains unknown. Once dredging is finished and lakes are accessible to the public, species diversity increases and this increase is likely associated with the (legal or illegal) introduction of small native cyprinids (e.g. *Rutilus rutilus, Abramis brama, Scardinius erythrophthalmus*) and popular sports fishing non-native species such as common carp (*Cyprinus carpio*), largemouth bass (*Micropterus salmoides*) and pikeperch (*Sander lucioperca*). Afterwards and as human use intensity increases, non-native species with no angling interest (usually legally classified as invasive) are observed included black bullhead (*Ameiurus melas*) and pumpkinseed (*Leppomis gibbosus*) (Zhao et al. 2016). Therefore, colonization history, management practices and environmental heterogeneity (e.g., lake size: mean = 12.33 ha ± 7.02 SD; min = 0.75 ha; max = 21.16 ha) among lakes promoted the existence of different fish communities and resulted in a strong gradient of dominance of non-native species.

Fish communities were sampled in each lake in 2012 and 2013 with one lake being sampled per day from mid-September to mid-October [see further details in Zhao et al. (2016)]. The same set of complementary passive (gillnetting with 2 and 4–6 nets in the pelagic and littoral habitats, respectively, spanning different types of microhabitats) and active (Point Abundance Sampling by Electrofishing, an effective sampling method for different fish species and life-stages in shallow littoral habitats) techniques were used in all lakes. All captured individuals were identified to the species level (except young-of-the-year bream, see below) and measured for fork length (i.e., length of a fish measured from the tip of the snout to the posterior end of the middle caudal rays) to the nearest mm, which is the most reproducible method of measuring fish (Kahn et al. 2004). The mass of each sampled individual was subsequently estimated using length/weight relationships for each species obtained when quantifying functional traits (see details below). These values were then used to compute the relative biomass of each species and the relative biomass of all non-native species in each community.

Functional traits of fish functional entities

A total of 25 fish species (13 native and 12 non-native) were sampled in the 18 lakes. As ontogenetic change in morphology is expected to be the most important driver of fish intraspecific variability, we defined three functional entities based on life-stages (i.e., young-of-the-year (YOY), juvenile or adult; further details available in Table 1) for each species. Individuals were grouped into functional entities according to their body size (i.e., fork length) and information from the literatures about age at maturity in the study area for each fish species (Keith et al. 2011; Froese and Pauly 2014). This classification yielded to a total of 56 functional entities (28 native and 28 non-native entities). Some species were represented by less than three functional entities because some of the life-stages were absent in sampled lakes (e.g. European eel, *Anguilla anguilla*).

Five ecological functions (i.e., food acquisition, locomotion, nutrient processing, reproduction and defense against predation) are associated with fish and could be described using relevant functional traits (Villéger et al. 2017). In the present study, we focused on two key functions (i.e., food acquisition and locomotion: e.g. Mason et al. 2008; Villéger et al. 2010; Albouy et al. 2011; Montaña et al. 2014; Leitão et al. 2016) and profiled them through morphology-based functional traits (Villéger et al. 2017). Following Villéger et al. (2010) and Zhao et al. (2014), a set of 16 functional traits computed as ratios between morphological measures were obtained through direct measurements on the specimens and photography-based analyses (Table 2). These functional traits were measured on a total of 1101 individuals used to describe the 56 entities observed in the regional pool. On average 20 (± 18 SD) individuals were described for each functional entity. These individuals originated mainly from field sampling in the studied lakes but, for some rare species, additional individuals were collected from other scientific surveys, from aquaculture, natural fish kills and local angling agencies in the study area.

Statistical analyses

To quantify functional diversity, a multidimensional functional space was built using a principal component analysis (PCA) based on scaled functional traits values of functional entities (mean of 0 and a standard deviation of 1; Villéger et al. 2008). The first four synthetic principal components of the PCA (PC1 = 26.0%, PC2 = 20.3%, PC3 = 13.5% and PC4 = 7.9%, respectively; Electronic Supplemental Material, Table S1) were kept to build the functional space where all the entities present in the regional pool were placed. These four PC axes accounts for 67.7% of the initial inertia in trait values and produce a mean-squared deviation index of 0.002, demonstrating that this functional space accurately represent the initial distances between functional entities (Maire et al. 2015).

Table 1 List of native and non-native fish species (common name, scientific name and code) and body size limits (length from snout to fork of caudal fin in mm) used to define functional entities within each species based on life stages (YOY: young-of-the-year, Juvenile and Adult) (adapted from Zhao et al. 2016)

Common name	Scientific name	Code	Size class used to define functional entities		
			YOY	Juvenile	Adult
Native					
Barbel	*Barbus barbus*	bab	n.a.	n.a.	> 160
Bitterling	*Rhodeus amarus*	rha	< 63	§	> 63
Bleak	*Alburnus alburnus*	ala	55–110	§	> 110
Bream spp.	*Abramis brama*	bre	< 135	135–210	> 210
	Blicca bjoerkna				210–380
Chub	*Squalius cephalus*	sqc	< 110	110–200	> 200
European eel	*Anguilla anguilla*	ana	n.a.	n.a.	> 330
European perch	*Perca fluviatilis*	pef	< 110	110–180	> 180
Gudgeon	*Gobio gobio*	gog	< 90	§	> 90
Northern pike	*Esox lucius*	esl	< 275	275–400	> 400
Roach	*Rutilus rutilus*	rur	< 100	100–150	> 150
Rudd	*Scardinius erythrophthalmus*	sce	< 90	90–120	> 120
Tench	*Tinca tinca*	tit	< 100	100–250	> 250
Nonnative					
Black bullhead	*Ameiurus melas*	amm	< 85	85–130	> 130
Common carp	*Cyprinus carpio*	cyc	< 200	200–400	> 400
European catfish	*Silurus glanis*	sig	< 200	200–900	> 900
Grass carp	*Ctenopharyngodon idella*	cti	n.a.	n.a.	> 460
Largemouth bass	*Micropterus salmoides*	mis	< 106	106–211	> 211
Mosquitofish	*Gambusia holbrooki*	gaa	< 30	§	> 30
Pikeperch	*Sander lucioperca*	sal	< 200	200–370	> 370
Prussian carp	*Carassius gibelio*	cag	< 160	160–250	> 250
Pumpkinseed	*Lepomis gibbosus*	leg	< 70	70–90	> 90
Rainbow trout	*Oncorhynchus mykiss*	onm	n.a.	n.a.	> 200
Ruffe	*Gymnocephalus cernua*	gyc	< 55	55–105	> 105
Silver carp	*Hypophtalmichthys molitrix*	hym	n.a.	n.a.	> 520

Functional entities were defined only for those size classes sampled in the studied lakes

n.a. indicates that the life stage was not observed in the sampled lakes

§ indicates that YOY and juveniles were pooled together

Functional differences between native and non-native entities

To investigate the extent of intraspecific functional variability relative to interspecific functional variability, we determined for each functional entity the identity of its nearest neighbor in the four-dimensional functional space based on Euclidean distances. The identity of the nearest neighbors was classified into three categories: same species, different species but same status (i.e., native or non-native) or different species and different status. Magnitude and intraspecific and interspecific functional variability were compared using the variation partitioning method provided by Taudiere and Violle (2016) applied on coordinates of functional entities on each PCA axis. This method assesses how much of the total variance among functional entities coordinates is due to variance within species and between species. We also calculated the percentage of each category of nearest neighbor for the whole pool of entities and within each lake fish community (i.e., accounting only for the functional entities present in a lake).

Next, to test for the existence of significant functional differences between all native and all non-native fish entities observed in the studied lakes, we used two complementary approaches. First, we used Permutational Multivariate Analysis (PERMANOVA, 9999 permutations; Anderson 2001) to assess whether position of native and non-native entities differed within the functional space. Second, we tested whether functional richness differed between the pools of native and non-native entities. We calculated the observed functional richness (defined as the volume of the convex hull shaping the entities in the multidimensional functional space) of native and non-native entities (Villéger et al. 2008). Then, a bootstrap

Table 2 List of the 16 functional traits measured on all fish individuals

Functional traits	Measure	Ecological meaning
Mass (F/L)	$\log(M+1)$	Volume, muscle mass
Oral gape surface (F)	$\frac{Md}{Mw}$	Maximum prey size or ability to filter water
Oral gape shape (F)	$\frac{Mw\times Md}{Bw\times Bd}$	Prey shape and food acquisition
Oral gape position (F)	$\frac{Mo}{Hd}$	Position of prey in the water
Eye diameter (F)	$\frac{Ed}{Hd}$	Prey detection
Gill raker length (F)	$\frac{Gl}{Bl}$	Filtration capacity or gill protection
Gut length (F)	$\frac{GRl}{Hd}$	Digestibility of food
Eye position (L)	$\frac{Eh}{Hd}$	Position in the water column
Body section shape (L)	$\frac{Bd}{Bw}$	Position in the water column and hydrodynamism
Body section area (L)	$\frac{\mathrm{In}\left(\left(\frac{\pi}{4}\times Bw\times Bd\right)+1\right)}{\mathrm{In}(M+1)}$	Mass distribution along the body and hydrodynamism
Pectoral fin position (L)	$\frac{PFi}{PFb}$	Maneuverability and position in the water column
Pectoral fin shape (L)	$\frac{PFl^2}{PFs}$	Propulsion and/or maneuverability
Caudal peduncle throttling (L)	$\frac{CFd}{CPd}$	Swimming endurance
Caudal fin shape (L)	$\frac{CFd^2}{CFs}$	Endurance, acceleration and/or maneuverability
Fins area ratio (L)	$\frac{2\times PFs}{CFs}$	Swimming type (pectoral or caudal fin propulsion)
Fins area (L)	$\frac{(2\times PFs)+CFs}{\frac{\pi}{4}\times Bw\times Bd}$	Endurance, acceleration and/or maneuverability

The letter in brackets indicates the function associated with each trait (F: food acquisition and L: locomotion). Adapted from Villéger et al. (2010) and Zhao et al. (2014)

M mass, *Bl* standard body length, *Bd* body depth, *CPd* caudal peduncle minimal depth, *CFd* maximal caudal fin depth, *CFs* caudal fin surface, *Ed* eye diameter, *Eh* distance between the center of the eye to the bottom of the head, *Gl* total gut length, *GRl* maximal gill raker length, *Hd* head depth along the vertical axis of the eye, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis, *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; *Bw* body width, *Md* mouth depth, *Mw* mouth width

procedure (10,000 randomizations) was used to calculate the expected functional richness of a random pool of 28 functional entities (i.e., number of entities observed for each status). Finally, we compared these expected functional richness values to the observed functional richness of native and non-native functional entities using Standardized Effect Size (SES) and *P* value.

In addition, we also calculated the level of functional overlap between all native and all non-native fish entities. Functional overlap (FOve) was calculated following Villéger et al. (2013) as the percentage of functional space shared by native and non-native entities based on the formula:

$$FOve=\frac{FRic(NN\cap N)}{FRic(N)+FRic(NN)-FRic(NN\cap N)},$$

where $FRic(N)$ is the convex hull volume of native entities, $FRic(NN)$ is the convex hull volume of non-native fish and $FRic(NN\cap N)$ is the volume of the intersection of the convex hulls of native and of non-native entities. A functional overlap value close to one indicates a high functional similarity (including similar functional richness and similar position in the functional space) between native and non-native entities.

Functional diversity along the level of dominance by non-native species

To identify how functional diversity varies among communities that differ in the degree of dominance by non-native species, we computed the functional richness for each lake fish community (i.e., including native and non-native species). We also included a set of functional diversity indices describing complementary facets of the filling of the functional space and accounting for species relative abundances. These indices were: functional evenness (FEve, the regularity of abundance distribution among strategies within a local community); functional divergence (FDiv, the proportion of abundance made by species with the most extreme strategies within a local community), and functional specialization (FSpe, the proportion of abundance for the most extreme strategies in the regional pool) (Mouillot et al. 2013). All functional diversity indices were calculated based on the average abundances of species across the two sampling years, as no significant change in fish community composition was observed between years (Zhao et al. 2016).

We then assessed whether these indices varied along the level of dominance by non-native species (i.e., defined as the relative biomass of non-native species in the lake fish communities) using linear regressions. To account for the fact that the relationship may be either monotonic (linear) or non-monotonic (hump-shape and *U* shape), we included a quadratic term in all the models that were subsequently retained only if significant ($P < 0.05$; Crawley 2007).

To test whether incorporating intraspecific variability could provide a better identification of how functional diversity varies among communities with contrasted dominance by non-native species, we repeated the same set of analyses but dividing each species into different functional entities (i.e., life-stages). When required, functional indices were box-cox transformed prior to the analyses to meet assumptions of linear models. All statistical analyses were conducted in R 3.2.2 (R development Core Team 2011).

Results

Fish species richness was highly variable among the studied lakes ranging from 3 to 15, with number of native species ranging from 0 to 8 (average 4.1 ± 1.9 SD) and number of non-native species ranging from 0 to 8 (average 3.8 ± 2.3 SD). Furthermore, the relative biomass of non-native fishes ranged from 0 to 100% (mean = 43.5% ± 33.1% SD), demonstrating that lakes markedly differed in the degree to which non-native species dominated the fish assemblage. The number of native and non-native entities ranged from 0 to 16 (mean = 8.7 ± 4.0 SD) and 0 to 15 (mean = 7.3 ± 4.7 SD), respectively. The taxonomic richness of fish was the highest in lakes that showed an intermediate degree of dominance by non-native species (Fig. 1). Lake productivity (concentration of Chlorophyll *a*) was not a significant driver of the four diversity indices (i.e., total number of species and of entities, and number of non-native species and number of entities; Table S2).

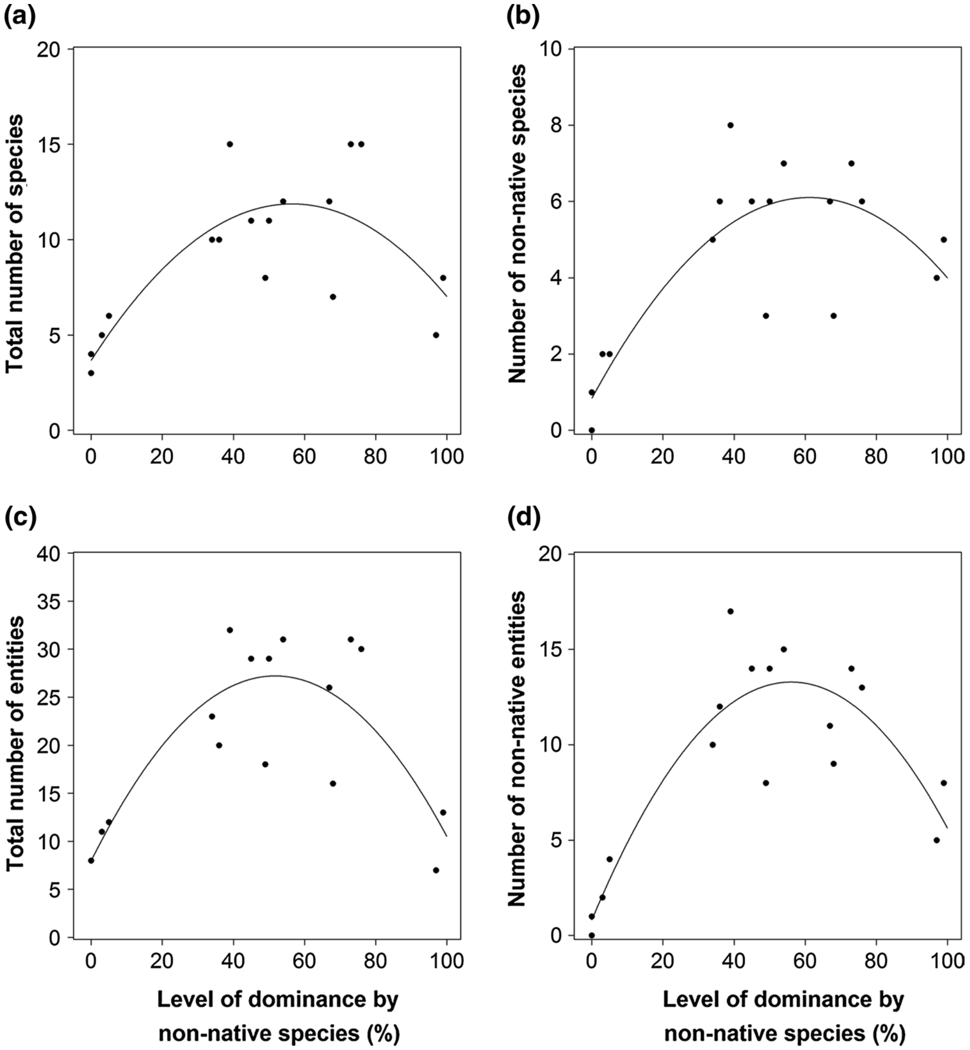

Fig. 1 Relationships between level of dominance by non-native species (% of biomass belonging to non-native species) and total number of species (**a**), total number of functional entities [defined as life-stages of each fish species; i.e., young-of-the-year (YOY), juveniles and adults; **c**] or number of non-native species/entities (**b** and **d**) in 18 lakes. Solid lines are the fitted relationships using linear models including a quadratic term ($P < 0.001$)

Intraspecific functional variability

In the regional pool, 51.8% of functional entities had their nearest neighbor belonging to the same species (e.g., the nearest neighbor of adults of species A were YOY or juveniles of species A), 32.1% were closest to an entity sharing a similar status but belonging to a different species and 16.1% belonging to a different species and status (Fig. 2, see further details in Electronic Supplemental Material, Table S3 and Fig. S1). Intraspecific variability (i.e., variability among functional entities) on each PCA axis accounted for 12% to 36% of the total variability (mean = 24.36% ± 8.05% SD). The importance of intraspecific variability was also observed within each studied lake. Specifically, nearest entities belonging to the same species accounted for only 44.4% (± 14.85 SD) of pairwise comparisons while those belonging to different species accounted for 55.6% (± 14.85 SD), with 33.1% (± 11.25 SD) corresponding to a similar status and 22.6% (± 14.23 SD) to a different status.

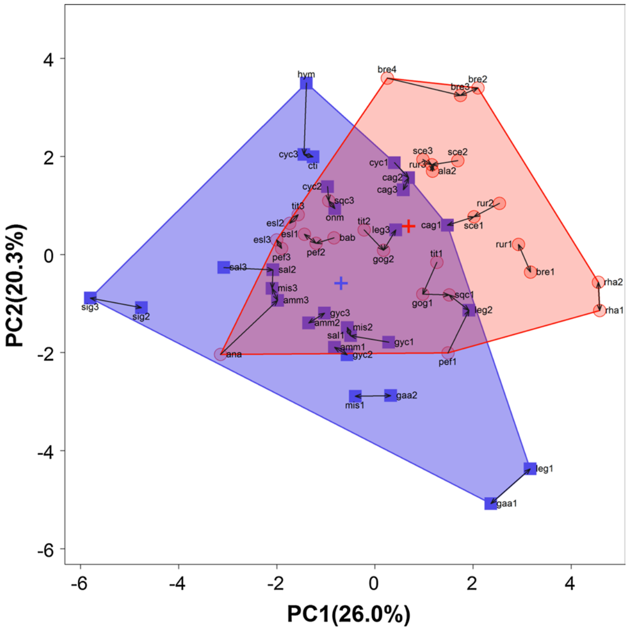

Fig. 2 Distribution of the functional entities [defined as life-stages of each fish species; i.e., young-of-the-year (YOY), juveniles and adults] in the functional space defined by the regional pool based on the two first PCA axes. Native ($n = 28$) and non-native ($n = 28$) entities are plotted in red circles and blue squares, respectively. Colored surfaces correspond to the functional richness and crosses to the center of gravity of the convex hulls. Arrows indicate the pairwise nearest neighbors of each entity. Codes of functional entities are available in Table 1 and the other axes combinations in Electronic Supplemental Material (Fig. S1). The same three first letters indicate entities belonging to the same species

Functional differences between native and non-native fish

Native and non-native entities filled different portions of the functional space (PERMANOVA, $P < 0.001$; Fig. 2). In addition, although they were composed of the same number of functional entities ($n = 28$), the observed functional richness of native entities (26.7% of the total functional space) was smaller than the richness of non-native entities (36.9%). Functional richness of native entities was also significantly smaller (SES = − 1.99, $P = 0.008$) than expected by chance while the functional richness of non-native entities did not differ from a random sampling (SES = − 1.17; $P = 0.114$). Functional overlap (FOve) was only 10.7%, indicating a limited functional similarity between native and non-native entities.

Functional diversity along the gradient of non-native species

The functional diversity of lake fish communities displayed significant changes along the gradient of non-native species (Fig. 3). When computing the different functional indices at the species level (i.e., without incorporating intraspecific functional variability; Table 3, Fig. 3), FRic values displayed a significant hump-shape curve ($R^2 = 0.54$, linear term: $P = 0.001$, quadratic term: $P = 0.003$) along the level of dominance by non-native species, with the highest value found at intermediate levels. FSpe displayed a significant linear increase ($R^2 = 0.50$, $P < 0.001$), indicating that biomass of functional specialists (i.e., species with the most extreme functional trait values) increased along the level of dominance by non-native species. No significant relationship was found between FEve or, FDiv and the level of dominance by non-native species ($P = 0.285$ and $P = 0.596$, respectively).

Incorporating intraspecific functional variability revealed functional diversity patterns contrasting with those found when accounting only for interspecific variability (Fig. 4). FRic values increased linearly along the level of dominance by non-native species ($R^2 = 0.42$, $P = 0.002$). Similarly, FEve and FSpe showed a significant linear increase ($R^2 = 0.35$, $P = 0.005$ and $R^2 = 0.43$, $P = 0.002$, respectively), indicating that both regularity of abundance distributions in the functional space and abundance of functional specialists increased. FDiv displayed a *U* shape curve, albeit only marginally significant ($R^2 = 0.23$, linear term: $P = 0.053$, quadratic term: $P = 0.058$), with the lowest values observed at intermediate perturbation levels (Table 4, Fig. 3). This indicated that intermediate level of dominance of non-native species was associated with the lowest abundance of functional specialists compared to functional generalists (i.e., species close to the center of the functional space).

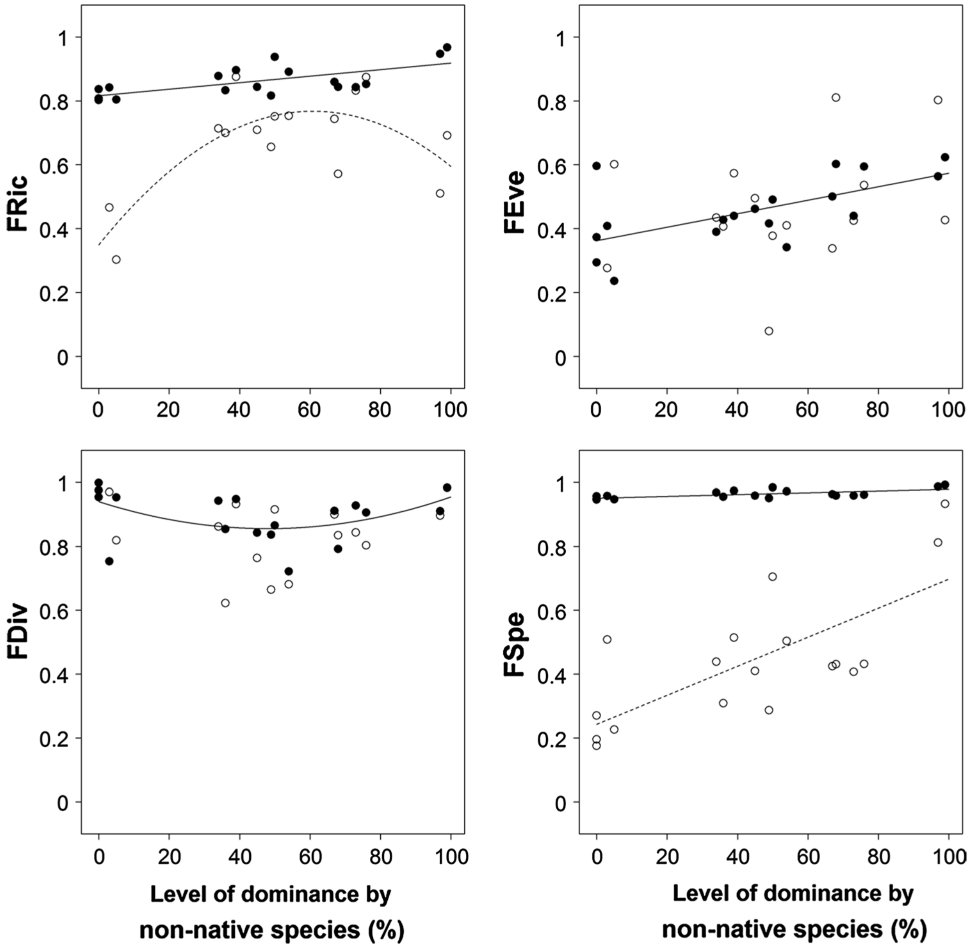

Fig. 3 Relationships between functional diversity indices (*FRic* functional richness, *FEve* functional evenness, *FDiv* functional divergence, *FSpe* functional specialization) and the level of dominance by non-native species (% of biomass belonging to non-native species). Filled dots indicate diversity indices computed at the functional entity level (incorporating intraspecific variability; $n = 18$), while open dots indicate functional diversity indices computed at the species level (without incorporating intraspecific variability; $n = 18$). Solid (entity level) and dotted (species level) lines represent significant relationships ($P < 0.05$)

Table 3 Results of the models used to test the covariation between functional diversity indices (FRic: functional richness; FEve: functional evenness; FSpe: functional specialization; FDiv: functional divergence) computed using average trait-values of species (i.e., all life-stages combined) and non-native species dominance

Response variables	Source of variation	d.f.	Estimate (SE)	*t*	*P*
FRic	Level of dominance by non-native species	12	1.37 (0.33)	4.18	**0.001**
	Level of dominance by non-native species^2	12	− 1.13 (0.31)	− 3.69	**0.003**
	Intercept	12	0.35 (0.08)	4.21	**0.001**
FEve	Level of dominance by non-native species	13	0.20 (0.18)	1.11	0.285
	Intercept	13	0.36 (0.10)	3.47	**0.004**
FDiv	Level of dominance by non-native species	13	0.06 (0.11)	0.54	0.596
	Intercept	13	0.80 (0.06)	12.60	**< 0.001**
FSpe	Level of dominance by non-native species	16	0.45 (0.11)	4.21	**< 0.001**
	Intercept	16	0.24 (0.06)	4.14	**< 0.001**

Significant effects are indicated in bold

Discussion

Our results demonstrated that functional diversity varied predictably with the degree to which non-native species dominated a fish assemblage in temperate lake fish communities. The present study also indicated that the patterns of variation of functional diversity could be different, and even missed, when intraspecific variability of functional traits was not accounted for. We found that intraspecific variability should not be omitted, with more than 10% of total variability in fish functional trait values being within the 25 studied fish species. Notably, we observed that about half of the functional entities (i.e., YOY, juvenile and adult life-stages) were not functionally close to a functional entity belonging to the same species. For instance,

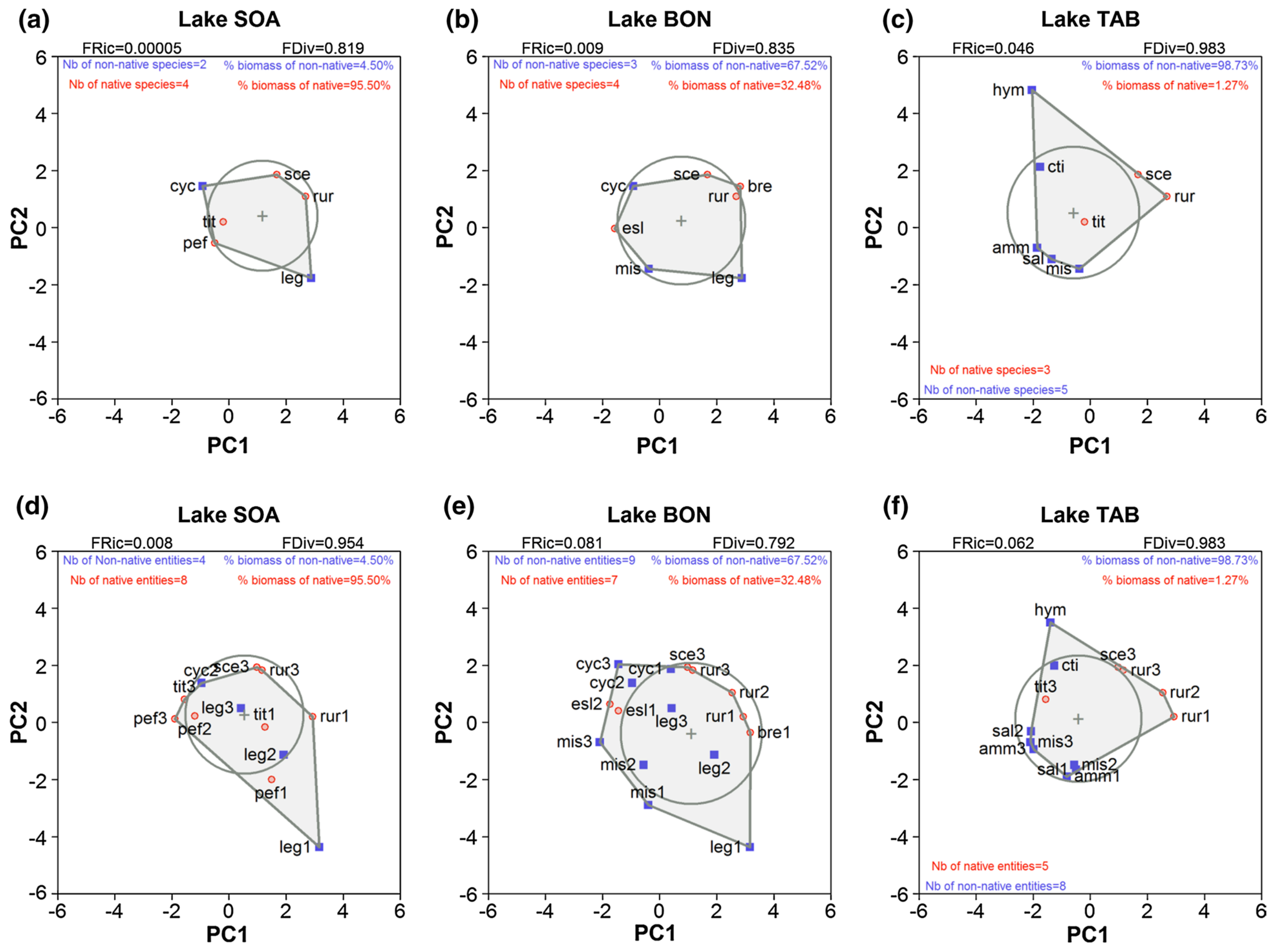

Fig. 4 Distribution of fish species (**a**, **b** and **c**) or functional entities [defined as life-stages of each fish species; i.e., young-of-the-year (YOY), juveniles and adults; **d**, **e** and **f**] in the functional space (only the two first PCA axes are shown), in three lakes with contrasted level of dominance by non-native species (i.e., contribution to fish biomass): low (**a** and **d**), medium (**b** and **e**), and high (**c** and **f**). Native and non-native entities are plotted in red circles and blue squares, respectively. Codes of functional entities are available in Table 1. The convex hull (light grey enclosed area) illustrates functional richness (FRic). The circle illustrates mean distance to the center of gravity of the convex hull (cross). The higher the proportion of biomass far from the center of gravity, the higher the functional divergence (FDiv). Values of functional richness (FRic) and functional divergence (FDiv) for each lake are given above each panel. Number (Nb) of native and non-native species/entities and contribution of native and non-native species to total fish biomass are given on the top or bottom of each panel

Table 4 Results of the models used to test the covariation between functional diversity indices (FRic: functional richness; FEve: functional evenness; FSpe: functional specialization; FDiv: functional divergence) computed using average trait values of functional entities (i.e., up to 3 life-stages within each species, Table 1) and non-native species dominance

Response variables	Source of variation	d.f.	Estimate (SE)	*t*	*P*
FRic	Level of dominance by non-native species	16	0.10 (0.03)	3.68	**0.002**
	Intercept	16	0.82 (0.02)	54.08	**< 0.001**
FEve	Level of dominance by non-native species	16	0.21 (0.07)	3.21	**0.005**
	Intercept	16	0.36 (0.04)	10.11	**< 0.001**
FDiv	Level of dominance by non-native species	15	− 0.35 (0.17)	− 2.10	**0.053**
	Level of dominance by non-native species^2	15	0.37 (0.18)	2.06	**0.058**
	Intercept	15	0.58 (0.05)	11.16	**< 0.001**
FSpe	Level of dominance by non-native species	16	0.03 (0.01)	3.70	**0.002**
	Intercept	16	0.95 (0.00)	229.41	**< 0.001**

Significant effects are indicated in bold the functionally closest entity of adult bleak (*Alburnus alburnus*; native) among all studied species was juvenile rudd (*Scardinius erythrophthalmus*; native). In addition, in 16% of the cases, the highest functional similarity was found between fish with different status (i.e., native *vs.* non-native), such as between adult northern pike (*Esox lucius*; native) and adult pikeperch (non-native) (Fig. 2). Functional similarities between entities from different species were also detected in lake fish communities where only a subset of species from the regional pool was present. For instance, non-native juvenile pumpkinseed (*Lepomis gibbosus*) and YOY of native European perch (*Perca fluviatilis)* were among the functionally closest entities (Fig. 4d). Similarly, non-native adult largemouth bass were very close to YOY of native northern pike (Fig. 4e). Accordingly, this high level of intraspecific variability coupled with some functional similarities between life-stages from different species resulted in blurred or even missed the patterns of functional diversity when accounting only for interspecific trait differences (Fig. 3, Tables 3 and 4). This is consistent with previous studies showing that the omission of intraspecific variability could cause a biased assessment of impacts of human perturbations on biodiversity (Cianciaruso et al. 2009; de Bello et al. 2011) and reinforce the claims that trait-based approaches should more often account for intraspecific variability (Bolnick et al. 2011; Albert et al. 2012; Violle et al. 2012).

In the present study, we observed that more fish species/entities were present at intermediate level of dominance by non-native fish (expressed as a percentage of biomass, Fig. 1), which is consistent with intermediate disturbance hypothesis (Roxburgh et al. 2004; Shea et al. 2004). This result suggests that (i) when lakes are dominated by non-native species, this is driven by a limited number of species and that (ii) at the intermediate disturbance level, ecological differences between species might allow the coexistence of species with variable levels of competitiveness (Roxburgh et al. 2004). This can be attributed to significant differences in functional traits between native and non-native fish. The low functional overlap between native and non-native fish was primarily driven by a few native entities being closer to non-native rather than to other native entities, such as European eel, YOY European perch and adult northern pike (Fig. 2, Electronic Supplemental Material, Table S2, Fig. S1). These results indicated that native and non-native fish strongly differed in their functional attributes, with non-native fish displaying unique and more diversified combinations of functional traits. This complementary functional space occupied by native and non-native fish can be due to the low richness of native fish species in gravel pit lakes (Zhao et al. 2016), which potentially provides more "empty" functional space for non-native species. The existence of such an ecological dissimilarity between non-native and native species suggested that being functionally different increased establishment success either because of human preferences for these unique attributes and/or because it conferred competitive advantages (Ordonez et al. 2010).

Non-native fish species can be both functionally close to native fish and extended beyond the native functional space (Pool et al. 2010), suggesting that non-native species can either effectively compete with native species or take advantage of additional niches that were unoccupied by native species. Given that framework and the specificity of artificial ecosystems, we argue that new interactions between native and non-native fish might occur within novel ecosystems to create a different structure for the fish communities, providing a unique opportunity to assess community assembly rules (Turgeon et al. 2016).

We also found that the variation of facets of functional diversity was even more marked when accounting for the diversity among their life-stages. Specifically, functional richness increased significantly with the level of dominance by non-native species. This is not surprising as lakes with higher biomass of non-native species are likely to host more species and/or more functional entities (e.g. both small and large individuals of a single species) and hence more extreme trait values (Stachowicz and Tilman 2005), since non-native species have functional attributes differing from those of native fishes (Fig. 2). In addition to functional richness, functional evenness and specialization of lake fish communities increased with the degree to which non-native species dominate the community. This is in stark contrast with previous studies that have observed a decrease in functional evenness when communities are facing other types of anthropogenic disturbances (e.g., habitat alteration, Villéger et al. 2010; Gerisch et al. 2012). In the studied lakes, a recent study has demonstrated that there was a unique community assembly process in gravel pit lakes with a gradual replacement of native fish by non-native fish as ecosystems become old (Zhao et al. 2016). Based on the results of the present study, this corresponds to a gradual replacement of functional generalists by functional specialists. As a result, non-native fish may benefit from exploiting new resources within the ecosystems. For instance, we observed that non-native European catfish displayed lower oral gape shape values (i.e., vertically flattened mouth) and higher pectoral fin position values (i.e., flapping-fin motion of lift-based swimming performance) than native species, which might enable them to consume large, energetically profitable prey items (Karpouzi and Stergiou 2003) and reach higher swimming speeds (Carol et al. 2007; Copp et al. 2009). Although the use of morphological functional traits to assess species diet (i.e., the realized trophic niche) has some limitations (Bellwood et al. 2006; Albouy et al. 2011), this approach can at least discriminate the potential scope of prey that species can consume (i.e., the fundamental trophic niche; Villéger et al.

2017). Within species, morphological functional traits are related to individual diet measured using stable isotope analyses and explained some of the trophic variability observed among individuals within a population (Zhao et al. 2014). More importantly, non-native fish may also improve their success possibility of colonization as increasing evenness of species abundance distribution in the functional space can avoid an increase in functional overlap (i.e., competition; Mason et al. 2008), and evasion of competition permitted coexistence based on the limiting similarity theory (Macarthur and Levins 1967).

Interestingly, nonlinear *U* shape curve relationship between functional divergence and the level of dominance by non-native species was also detected, indicating that abundance of functional specialists' distribution in trait space was the most skewed at the intermediate disturbance level (Table 3, Figs. 3 and 4). This can be explained by the interplay between two opposite processes along the level of dominance by non-native species, that is, the decrease in relative biomass of native specialists and the increase in relative biomass of non-native specialists. For instance, in the low (e.g., Lake SOA), medium (e.g., Lake BON) and high (e.g., Lake TAB) relative biomass of non-native species lakes, functional specialists occupied 80.77% (native), 56.99% (both native and non-native) and 88.97% (non-native) of the total biomass, respectively (Fig. 4d–f). Previous species–energy relationships indicated that more energy inputs were needed to support increasing abundance of specialized species in animal communities (Kaspari 2001; Evans et al. 2006; Tedesco et al. 2007). Our findings, combined with our previous study (Zhao et al. 2016), suggested that older and more productive gravel pit lakes are dominated by non-native fish species. This scenario can also be attributed to human commensal hypothesis indicating that non-native species can thrive in the presence of humans, probably because they are better adapted to highly disturbed human–environment (Jeschke and Strayer 2006; Buckley and Catford 2016). Since the level of dominance by non-native species we considered in the present study was a spatial instead of a temporal gradient, additional studies are needed to confirm our conclusions.

In conclusion, the present study demonstrated the unique community assembly process of native and non-native fish in gravel pit lakes by accounting for intraspecific functional variability. Beyond our studies, a critical question that ecologists need to answer in further studies is the dynamics of mixed assemblages of native and non-native species created by human use of heterogeneous landscapes (Gibson et al. 2015; Turgeon et al. 2016). Since the studied gravel pit lakes are under varying degrees of influences by humans (Zhao et al. 2016), we believe that this gradient of relative biomass of non-native species within these artificial lakes can allow us to better understand how mixed assemblages are structured. Furthermore, we confirmed that non-native fish were significantly different from native fish in terms of functional attributes, which eventually mediate the level of covariation of functional diversity with non-native fish dominance in fish assemblages. Because morphology-based functional diversity is expected to be related to ecosystem functioning (Rudolf 2012; Gagic et al. 2015; Lefcheck and Duffy 2015), future studies should focus on assessing how reported covariation between functional diversity and non-native species dominance might affect the trophic structure of communities and ecosystem functioning.

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Author contribution statement JC, SV and ZT designed the study. TZ acquired and analyzed the data, wrote the first draft of the manuscript. All authors originally formulated the idea, developed the methodology, and contributed to revisions.

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