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Trait structure and redundancy determine sensitivity to disturbance in marine fish communities

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Abstract

Trait diversity is believed to influence ecosystem dynamics through links between organismal traits and ecosystem processes. Theory predicts that key traits and high trait redundancy—large species richness and abundance supporting the same traits—can buffer communities against environmental disturbances. While experiments and data from simple ecological systems lend support, large-scale evidence from diverse, natural systems under major disturbance is lacking. Here, using long-term data from both temperate (English Channel) and tropical (Seychelles Islands) fishes, we show that sensitivity to disturbance depends on communities' initial trait structure and initial trait redundancy. In both ecosystems, we found that increasing dominance by climatically vulnerable traits (e.g., small, fast-growing pelagics/corallivores) rendered fish communities more sensitive to environmental change, while communities with higher trait redundancy were more resistant. To our knowledge, this is the first study demonstrating the influence of trait structure and redundancy on community sensitivity over large temporal and spatial scales in natural systems. Our results exemplify a consistent link between biological structure and community sensitivity that may be transferable across ecosystems and taxa and could help anticipate future disturbance impacts on biodiversity and ecosystem functioning.

KEYWORDS

climate change, coral reefs, diversity stability, ecological traits, ecosystem functioning, English Channel, functional diversity

1 | INTRODUCTION

Global environmental changes are threatening the sustainability of ecosystem functions and services, with severe consequences for human livelihood and well-being (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Cheung, Reygondeau, & Frölicher, 2016; Mora et al., 2015; Smith & Myers, 2018). It is therefore crucial to understand how variation in biodiversity may influence the sensitivity of communities and ecosystems to environmental change (Beaugrand, Edwards, Raybaud, Goberville, & Kirby, 2015;

Heilpern, Weeks, & Naeem, 2018; Nolan et al., 2018; Segan, Murray, & Watson, 2016). Species diversity has been shown to sustain ecosystem productivity and stability under environmental disturbances (Isbell et al., 2015; Liu et al., 2018; Mellin, Bradshaw, Fordham, & Caley, 2014; Schneider, Brose, Rall, & Guill, 2016). However, beyond species diversity, examining the diversity of organismal traits can provide a more mechanistic understanding of community dynamics via trait–environment relationships and through associated changes in ecosystem processes (Cadotte, 2017; Craven et al., 2018; Gross et al., 2017; Sakschewski et al., 2016).

Under the insurance (or redundancy) hypothesis, several species supporting similar key ecological roles (i.e., sharing similar ecological traits) should buffer communities against the impacts of environmental change (Dee et al., 2016; Díaz & Cabido, 2001; Laliberté et al., 2010; Nash, Graham, Jennings, Wilson, & Bellwood, 2016; Sanders, Thébault, Kehoe, & van Veen, 2018). Limited experimental and observational evidence over small temporal and spatial scales supports this theory. For instance, on coral reefs, key functions such as grazing and bio-erosion by large parrotfishes can maintain benthic community resilience following disturbances (Bozec, O'Farrell, Bruggemann, Luckhurst, & Mumby, 2016; Heenan, Hoey, Williams, & Williams, 2016; McLean, Cuetos-Bueno, Nedlic, Luckymiss, & Houk, 2016), and redundancy within parrotfish groups may reinforce these functions (Burkepile & Hay, 2008). In plant communities, higher trait redundancy has been linked to higher community stability in experimental plots exposed to grazing (Pillar et al., 2013). However, long-term empirical evidence demonstrating the buffering effects of trait redundancy in ecological communities is lacking.

The insurance hypothesis additionally suggests that community dynamics depend not only on environmental variation but also on the initial biological structure of communities. Indeed, the initial structure of communities can determine their successional trajectories under disturbance (Fukami, Martijn, Mortimer, & Putten, 2005; Williams et al., 2010), and two potential (nonmutually exclusive) biological mechanisms may explain differences in sensitivity among communities impacted by similar disturbances: (a) sensitive communities are more dominated by species with vulnerable traits (to a given disturbance) and/or (b) sensitive communities have lower trait redundancy (Walker, 1992; Williams et al., 2010). Thus communities' initial trait structure at a baseline time period (i.e., predisturbance) could determine communities' sensitivity or resistance to environmental disturbances (Barros, Thuiller, Georges, Boulangeat, & Münkemüller, 2016). Yet, while limited evidence supports the insurance hypothesis, no study has examined whether key traits or initial trait redundancy can buffer communities against environmental change in natural systems across large temporal and spatial scales.

Here, using multidimensional spaces based on species' ecological traits, we assessed whether community sensitivity was determined by initial trait structure or initial trait redundancy. Using long-term data from both temperate and tropical marine fish communities, we show that increased dominance by species with climatically vulnerable traits rendered communities more susceptible to environmental change, while communities with higher trait redundancy were more resistant, demonstrating the potential buffering capacity of trait redundancy in diverse, natural systems.

2 | MATERIALS AND METHODS

2.1 | Eastern English Channel: temperate marine fish communities

2.1.1 | Disturbance

The fish communities of the Eastern English Channel (EEC) experienced a major shift in both taxonomic and trait structure in 1997 in response to an Atlantic-wide climate oscillation (The Atlantic Multidecadal Oscillation) that led to rapid sea surface warming and oceanographic changes (Auber, Travers-Trolet, Villanueva, & Ernande, 2015; Ting, Kushnir, Seager, & Li, 2009). While all sampling sites throughout the EEC were concurrently impacted by a basin-wide climate disturbance, the magnitude of community change was highly variable among sites with some sites experiencing very pronounced shifts and others remaining more stable (Auber, Travers-Trolet, Villanueva, & Ernande, 2017).

2.1.2 | Fish community data

The fish community of the EEC (area VIId defined by the International Council for the Exploration of the Sea, ICES) has been sampled every October since 1988 during the scientific monitoring campaign named the Channel Ground Fish Survey (CGFS). Here, we focused on the study period of 1988–2011. The CGFS sampling scheme was spatially stratified by subdividing the EEC into 15′ longitude × 15′ latitude rectangles where at least one 30-min haul was made during daylight hours at an average speed of 3.5 knots. A high (3 m) vertical opening bottom trawl (GOV) with a 10-mm-stretched-mesh-size codend was used. After each haul, all captured fishes were identified and counted. Abundance indices at each sampling station were obtained from the ICES data portal and were standardized to numbers of individuals per km^2 (ICES). Because weather sometimes prevents sampling, sites with three or more consecutive years of missing data were removed, resulting in 79 total sampling sites. Before analyses, abundance data were $\ln(Ax + 1)$ transformed (where $A \times \min(x) = 2$; Auber et al., 2017; Van den Brink, Hattink, Bransen, Van Donk, & Brock, 2000) to reduce the influence of highly dominant species.

2.1.3 | Traits

Following the definition of Violle et al. (2007), we examined community dynamics not only through ecological traits related to energy transfer but also through traits related to environmental filtering and biological interactions like competition. More precisely, seven traits related to life history, habitat use, and trophic ecology were collected for 73 taxa (67 species, 6 identified to genera only). These included length and age at maturity, fecundity, offspring size, parental care, water column position, and trophic guild (Table S1). Trait data came from FishBase (Froese & Pauly, 2012), Engelhard, Ellis, Payne, ter Hofstede, and Pinnegar (2011), and Pecuchet et al. (2017). Traits encompassing life history, trophic ecology, and habitat preferences were chosen as they have known influences over species responses to environmental changes and influences on ecosystem processes (McLean et al., 2018; Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017). While some studies have recommended examining trait redundancy uniquely with "effect" traits, there is much overlap between "response" and "effect" traits in marine fishes, and traits used in this study have known links to ecosystem functioning (Villéger et al., 2017). For example, body size and age at maturity can determine species responses through differences in population turnover and generation time (Perry, Low, Ellis, & Reynolds, 2005), yet body size is a universal trait controlling mobility, feeding rate, and species interactions, hence impacts on trophic networks and nutrient cycles (Bellwood, Streit, Brandl, & Tebbett, 2019). Resource fluctuations and phenological mismatches can lead to shifts in trophic guild dominance (Hargeby, Andersson, Blindow, & Johansson, 1994; Thackeray et al., 2016), and trophic shifts can alter energy transfer and food web stability (Mumby et al., 2006). Water column position has not only been linked to changes in distribution and abundance because pelagic fishes have greater capacity for range shifts (Rijnsdorp, Peck, Engelhard, Möllmann, & Pinnegar, 2009), but also influences nutrient cycling and benthic–pelagic coupling (Griffiths et al., 2017).

2.1.4 | Environmental factors

We examined environmental factors known to drive fish community dynamics in marine ecosystems, including depth, sea surface temperature (SST), and salinity. Although the majority of species in the English Channel are demersal, SST was appropriate because the ecosystem is shallow (mean depth = 63 m) and well-mixed, and the majority of species have pelagic eggs and larvae, which are the most vulnerable life stages of marine fishes (Pepin, 1991). Depth was measured in situ during community sampling, SST data came from the kriging-interpolated Ifremer AVHRR/Pathfinder database (Saulquin & Gohin, 2010), and salinity data came from the NORWegian ECOlogical Model (NORWECOM), a coupled 3D physical/biochemical model of environmental factors for the North Sea and the English Channel (Skogen, Svendsen, Berntsen, Aksnes, & Ulvestad, 1995). Depth is a major driver of community structure in marine ecosystems as it influences light penetration, temperature and oxygen profiles, water column mixing, and habitat type. SST is a primary driver of species' distributions and abundances globally, and SST warming can profoundly impact marine fish communities, which are highly responsive to changes in temperature (Simpson et al., 2011). Salinity can influence community structure through physiological responses, impacts on larval success, and shifts between stenohaline and euryhaline species (Petereit et al., 2009; Sirot et al., 2015). Although chlorophyll-*a* can also determine community structure through bottom-up control and through larval success and recruitment (Beaugrand, 2004; Capuzzo et al., 2017), spatially resolved data for chlorophyll-*a* were not available prior to 1998. Spatially resolved data for fishing pressure were also unavailable prior to 2000; however, the rapid shift in fish communities in the English Channel was driven primarily by climate and not by fishing (Auber et al., 2015), and the objective of this study was to examine heterogeneity in community responses following the climatic disturbance.

2.2 | Seychelles Islands: coral reef-fish communities

2.2.1 | Disturbance

The Seychelles Islands experienced widespread coral mortality following severe coral bleaching during the 1998 El Niño that led to substantial changes in reef fish taxonomic and trait structure (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Graham et al., 2006). The mass bleaching was severe across the entire inner Seychelles (Graham et al., 2015, 2006), and of the 21 sites surveyed, all but one site had losses in coral cover, with an average 65% loss across all sites. Aside from the bleaching, there were no other large-scale disturbances in the inner Seychelles during this time frame, and other local stressors remained stable (Graham et al., 2006). While differential benthic trajectories following the mass bleaching have been linked to environmental and ecological conditions (Graham et al., 2015; Nash et al., 2016), variation in initial disturbance sensitivity has not yet been investigated.

2.2.2 | Fish community data

Fish abundance data were collected at 21 sites around the Seychelles Islands using underwater visual census in both 1994 (predisturbance) and 2005 (postdisturbance). At each site, 16 individual 7-m radius (154 m^2) stationary point counts were surveyed along the reef slope, and the identity and density of diurnally active, noncryptic reef fishes were recorded within each count (Graham et al., 2015, 2006). As with the EEC, abundance data were $\ln(Ax + 1)$ transformed before analyses.

2.2.3 | Traits

While intrinsic differences between the two study ecosystems lead to different trait choices, we attempted to maximize trait overlap between ecosystems. Life-history traits such as fecundity and offspring size are largely undescribed for coral reef fishes; however, length at maturity, age at maturity, and parental care were all available. Seven traits related to life history, habitat use, behavior, and trophic ecology were therefore collected for the 129 species sampled. These included length and age at maturity, parental care, water column position, trophic guild, mobility, and gregariousness (i.e., schooling behavior; Table S2). Trait data were collected primarily from FishBase (Froese & Pauly, 2012) and previously published literature (Graham et al., 2011, 2015; Stuart-Smith et al., 2013; Wilson et al., 2008), while length and age at maturity estimates were derived from the R package *FishLife* (Thorson, Munch, Cope, & Gao, 2017). These traits were chosen not only to maximize overlap between ecosystems but also because they have been previously implicated in reef fish responses to environmental change and influences on ecosystem processes (Graham et al., 2011; Pratchett et al., 2008; Stuart-Smith et al., 2013; Wilson et al., 2008). For example, body size and diet determine energy needs, predator–prey relationships, and trophic interactions, parental care determines habitat requirements and habitat modification, gregariousness influences predation vulnerability, nutrient cycling, and resource depletion, and mobility influences home range (i.e., scale of ecological role) and nutrient transfer (Mouillot et al., 2014; Stuart-Smith et al., 2013; Wilson et al., 2008).

2.2.4 | Environmental factors

We examined known environmental drivers of reef-fish community structure, including management status (i.e., openly fished sites vs. marine reserves), depth, coral cover, and reef complexity. Fishing is a primary driver of reef fish community structure and can erode diversity and ecosystem functioning, and thus openly fished sites could be more sensitive to disturbance than marine reserves (Cinner et al., 2018; Houk et al., 2015). Depth controls coral-reef structure through light attenuation and wave exposure (Bridge, Hughes, Guinotte, & Bongaerts, 2013) while coral cover and complexity can enhance habitat diversity and resource availability (Richardson, Graham, Pratchett, & Hoey, 2017; Rogers, Blanchard, & Mumby, 2014). Within each stationary point count, the percent cover of live hard coral was quantified and the structural complexity of the reef was visually estimated (Graham et al., 2006; Graham et al., 2015). Structural complexity was assigned to one of the five categories: 0 = no vertical relief, 1 = low (<30 cm) and sparse relief, 2 = low but widespread relief, 3 = widespread moderately complex (30–60 cm) relief, 4 = widespread very complex (60–100 cm), and 5 = exceptionally complex (>1 m) relief, which aligns with several other methods of assessing structural complexity on coral reefs (Wilson, Graham, & Polunin, 2007).

2.3 | Quantifying sensitivity

2.3.1 | Multidimensional trait space

We first generated a trait space for each ecosystem where species are arranged according to their trait values and distances between species reflect their trait similarity (Maire, Grenouillet, Brosse, & Villéger, 2015; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). We computed Gower dissimilarity matrices of the species by traits table for each ecosystem; Gower dissimilarity is well adapted for examining traits as it can handle multiple data types (i.e., continuous and categorical) and missing values (Gower, 1971). Trait spaces were then built by ordinating the Gower matrices using principal coordinates analysis (PCoA; Villéger, Mason, & Mouillot, 2008). For each ecosystem, we kept the first four axes of trait space, which cumulatively explained nearly 80% of total variance in both cases. Four axes have been shown to effectively capture community variation while maintaining initial Gower dissimilarity (Maire et al., 2015), and Mantel tests revealed that Euclidean distances between species in four-dimensional spaces were strongly correlated with initial Gower distances (EEC: $r = 0.96$, $p < 0.001$; Seychelles: $r = 0.96$, $p < 0.001$). Including additional axes did not greatly improve these relationships (six axes; EEC: $r = 0.98$; Seychelles: $r = 0.98$), demonstrating that the majority of variability in traits was accurately captured with four axes.

2.4 | Sensitivity

Using the trait space, we quantified “sensitivity” as the amount of change in trait structure following disturbance. Large shifts in trait structure indicate low resistance and thus high sensitivity, while small shifts indicate high resistance and low sensitivity. For a given ecosystem, we first calculated abundance-weighted community centroids in trait space for all sites in all time periods (Figure 1a). Within the trait space, the location of any given community in any given year is defined as the abundance-weighted centroid of all species in the community (Figure 1a). Thus, the movement of a community in the trait space can be used to quantify changes in trait structure through time. We therefore calculated sensitivity as the Euclidean distance between a community's position in trait space before and after disturbance (Figure 1b). This quantifies the amount of distance each community moved in trait space following a disturbance, where sites with larger movements display higher sensitivity and sites with smaller movements display higher resistance. In the EEC, where an abrupt shift occurred in the middle of a long time series, for each community, we calculated the distance between the average position of all years before and all years after the shift (1997), while in the Seychelles, for each site, we calculated the distance between 1994 (prebleaching) and 2005 (postbleaching).

2.5 | Trait redundancy

Redundancy quantifies the degree to which species in a community share similar ecological characteristics, that is, whether ecological roles are supported by few or many species and individuals. Multiple methods exist for calculating trait redundancy that are mostly based on deriving ecological groups or calculating distances between adjacent species in multidimensional space (Bruno, Gutiérrez-Cánovas, Sánchez-Fernández, Velasco, & Nilsson, 2016; Micheli & Halpern, 2005; Mouillot et al., 2014; Pillar et al., 2013; Ricotta et al., 2016). However, such indices require subjective choices such as the number of ecological groups or the cutoffs for nearest-neighbor calculations (e.g., nearest single neighbor vs. nearest five neighbors), and some indices only work with categorical traits (Bruno et al., 2016; Ricotta et al., 2016). Furthermore, most indices do not account for abundance or evenness, which can drastically impact trait redundancy as a higher number of individuals, not only species, supporting the same ecological role can provide greater buffering capacity against disturbances, and high evenness across species should lead to greater average redundancy than a community dominated by few species (D'agata, 2016). We therefore quantified trait redundancy following de

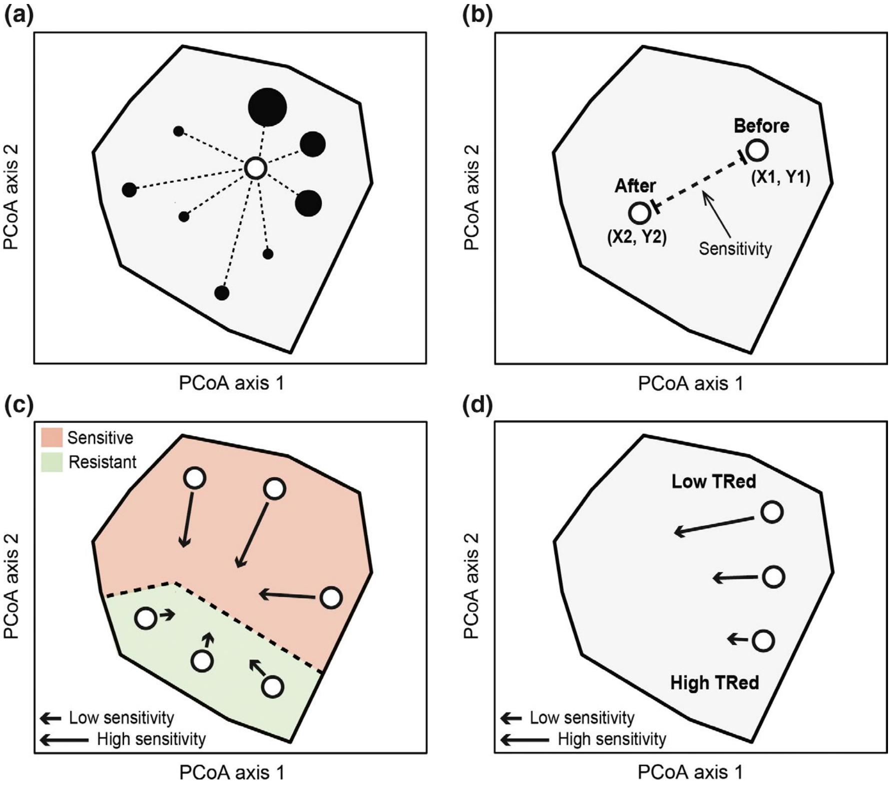


FIGURE 1 Conceptual diagrams showing the calculation of sensitivity according to changes in the abundance-weighted community position in trait space (a) following disturbance (b), along with potential links between (i) sensitivity and initial trait structure (c) and (ii) sensitivity and initial trait redundancy (TRed) (d). In (a) black circles represent species positions in trait space with sizes scaled by abundance and the white circle represents the abundance-weighted community centroid. Panel (b) shows sensitivity calculated as the distance moved in trait space following a disturbance. In (c) communities in the upper area of trait space have sensitive trait structures and exhibit large shifts (arrows), whereas communities in the lower area have resistant trait structures. In (d) communities with low trait redundancy exhibit large shifts (arrows), indicating high sensitivity, whereas communities with high trait redundancy exhibit resistance [Colour figure can be viewed at wileyonlinelibrary.com]

Bello, Lepš, Lavorel, and Moretti (2007) and Ricotta et al. (2016), where trait redundancy is defined as the degree to which a community is "saturated" with similar traits, and is calculated as the difference between taxonomic diversity (Simpson's index) and trait diversity (Rao's quadratic entropy). In this way, communities with the same level of trait diversity but different levels of taxonomic diversity (or vice versa) will vary in trait redundancy, where a community with either more ecologically similar species or higher species diversity will have higher redundancy (de Bello et al., 2007; Ricotta et al., 2016). Previous studies quantifying trait redundancy using this metric found significant relationships with community stability and environmental filtering, demonstrating the utility for examining relationships between redundancy and community dynamics while integrating species abundance distributions (Bruno et al., 2016; Kang et al., 2015; Pillar et al., 2013). Additionally, this metric of trait redundancy is calculated at the community level using continuous data, and does not require defining ecological groups. Initial trait redundancy (i.e., predisturbance) was calculated for all fish communities in both ecosystems using the R package *SYNCSA*.

2.6 | Generalized Linear Models

To consider the influences of environmental factors, for each site we calculated the change in each variable following disturbance (mean before vs. mean after) rather than using temporally averaged spatial variables, to avoid using static independent variables to predict dynamic dependent variables. Thus, changes in local environmental factors were used to predict changes in community trait structure. For instance, while the EEC was impacted by an Atlantic-wide climate oscillation and associated ocean warming, local-scale variability in SST or salinity change could explain variability in community responses. Depth was the only factor included in all statistical models, as it is a permanent environmental condition (on ecological time scales). Therefore, in the EEC, we built generalized linear models (GLMs, Gaussian distribution) testing the influences of (a) the initial position of each fish community in trait space (PCoA 1 and PCoA 2 scores), (b) initial trait redundancy, (c) species richness, (d) depth, (e) changes in local SST, and (f) changes in local salinity on community sensitivity. In the Seychelles, we used GLMs to test the influences of (a) the initial position of each fish community in trait space (PCoA 1 and PCoA 2 scores), (b) initial trait redundancy, (c) species richness, (d) depth, (e) percent change in coral cover, (f) percent change in reef structural complexity, and (g) management status on sensitivity. While sensitivity was calculated in four-dimensional space, only the first two PCoA axes were included in GLMs since they carry the majority of ecological-trait variation (>50%), and are thus sufficient to test the hypothesis that initial trait structure influences sensitivity. To identify the relative importance of independent variables, we used the *dredge* function from the R package *MuMin*, which calculates Akaike weights for each variable by comparing Akaike information criteria across the set of models containing all possible combinations of variables (Arruda Almeida, Green, Sebastián-González, & dos Anjos, 2018; Barton, 2019). Next, to assess the robustness of the relationships between sensitivity and independent variables, we re-ran the analyses using all combinations of six traits out of seven. For each model repetition, we calculated the corresponding Akaike weights, and independent variables were ranked according to their mean Akaike weights across all models (full model and all combinations of six traits). Finally, the full GLMs were checked for spatial autocorrelation by testing model residuals with Moran's *I*.

2.7 | Null models

To examine whether the relationships between sensitivity and (a) initial trait structure, or (b) initial trait redundancy were significantly different than expected by chance, we built null models examining the slope of the linear regression between sensitivity and each metric, following Fukami et al. (2005). For each null model, we randomly permutated species abundances (i.e., abundances were randomly shuffled between species), recalculated abundance-weighted community centroids in trait space, recalculated trait redundancy, and recomputed the corresponding linear models. This process was repeated 1,000 times and the corresponding linear models were used to build null distributions of 1,000 slopes. The actual observed slopes between sensitivity and (a) initial position in trait space, and (b) initial trait redundancy were then compared to the resulting null distributions.

3 | RESULTS

3.1 | Climatic disturbance in a temperate marine fish community

In the EEC, the first two axes of trait space captured 52% of overall variation in fish trait structure across the 73 taxa (Figure 2a), while the third and fourth axes explained an additional 24%. The first axis of trait space was primarily characterized by differences between large-bodied, long-lived species with large offspring (lower values) versus small-bodied, short-lived pelagic species and detritivores (higher values), while the second axis was characterized by differences between carcinophages and benthopiscivores with high parental care and large offspring (higher values) versus pelagic species, planktivores, and detritivores with low parental care and small offspring (lower values; Figure 2a; Figure S2). We found that the distance each community moved across the trait space following the disturbance was significantly correlated with the initial position of each community along the first and second axes of space, as communities with lower PCoA 1 and PCoA 2 values experienced higher changes in trait structure following the disturbance (PCoA 1: $r = -0.25$, $p < 0.05$; PCoA 2: $r = -0.27$, $p = 0.01$; Figures 2a,b and 3a; Figure S1). We found that distance moved was also significantly and negatively correlated with initial trait redundancy: fish communities with higher trait redundancy were more resistant and had less pronounced shifts ($r = -0.50$, $p < 0.0001$; Figure 3b). GLMs then ranked PCoA 2 position, trait redundancy, and local salinity changes as the most important variables predicting the distance moved by each community across the trait space (top 3 variables, Table 1), with secondary contributions by local temperature changes, depth, PCoA 1 position, and species richness. No spatial autocorrelation was found in the model residuals (Moran's *I*, $p = 0.41$), indicating the results were robust to spatial effects and that we did not omit major factors in the models.

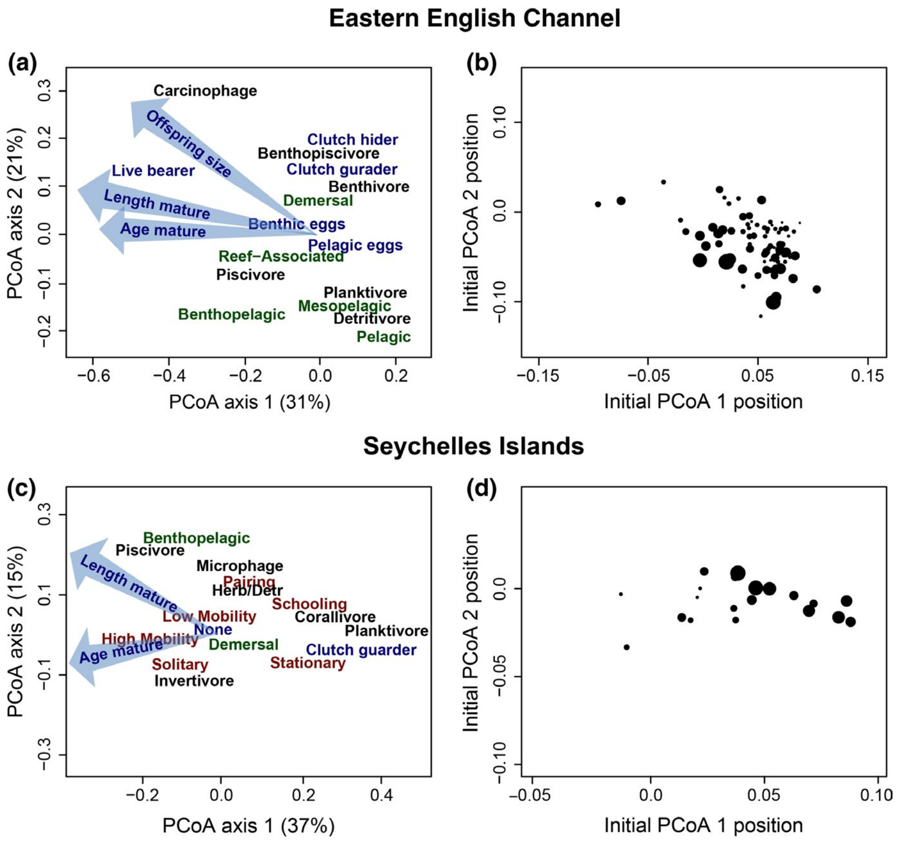


FIGURE 2 Trait space and sensitivity of fish communities in the Eastern English Channel (EEC) and Seychelles Islands. (a) Trait structure of the overall EEC fish community. (b) Sensitivity of fish communities in the EEC defined by the distance moved (i.e., amount of change) in trait space following disturbance; larger circles = higher movement and therefore higher sensitivity. (c) Trait structure of the overall Seychelles fish community. (d) Sensitivity of fish communities in the Seychelles defined by the distance moved in trait space following disturbance [Colour figure can be viewed at wileyonlinelibrary.com]

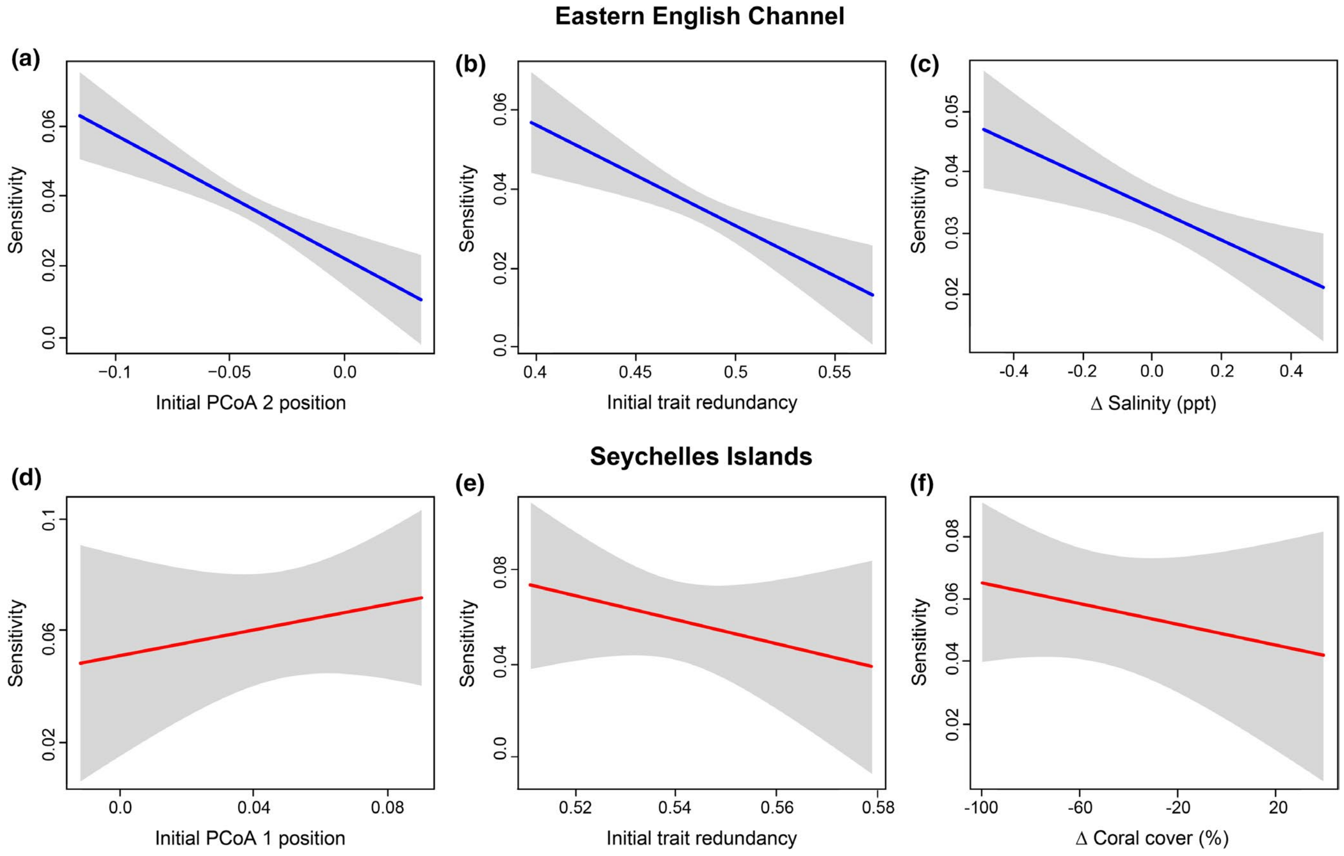


FIGURE 3 Partial relationships from generalized linear models (GLMs) between sensitivity and the most important explanatory factors in the Eastern English Channel (EEC) and Seychelles Islands. Relationships between sensitivity and (i) initial position on PCoA axis 2 of trait space (a), (ii) initial trait redundancy (b), and (iii) local salinity changes (c) in the EEC. Relationships between sensitivity and (i) initial position on PCoA axis 1 of trait space (d), (ii) initial trait redundancy (e), and (iii) coral cover change (f) in the Seychelles. Relationships were plotted using the inverse link function from GLMs via the R package *Visreg* [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Results of generalized linear models using Akaike weights to assess and rank the importance of independent variables in determining sensitivity. Akaike weight means and standard deviations were derived across all models (full model of seven traits and all combinations of six out of seven traits)

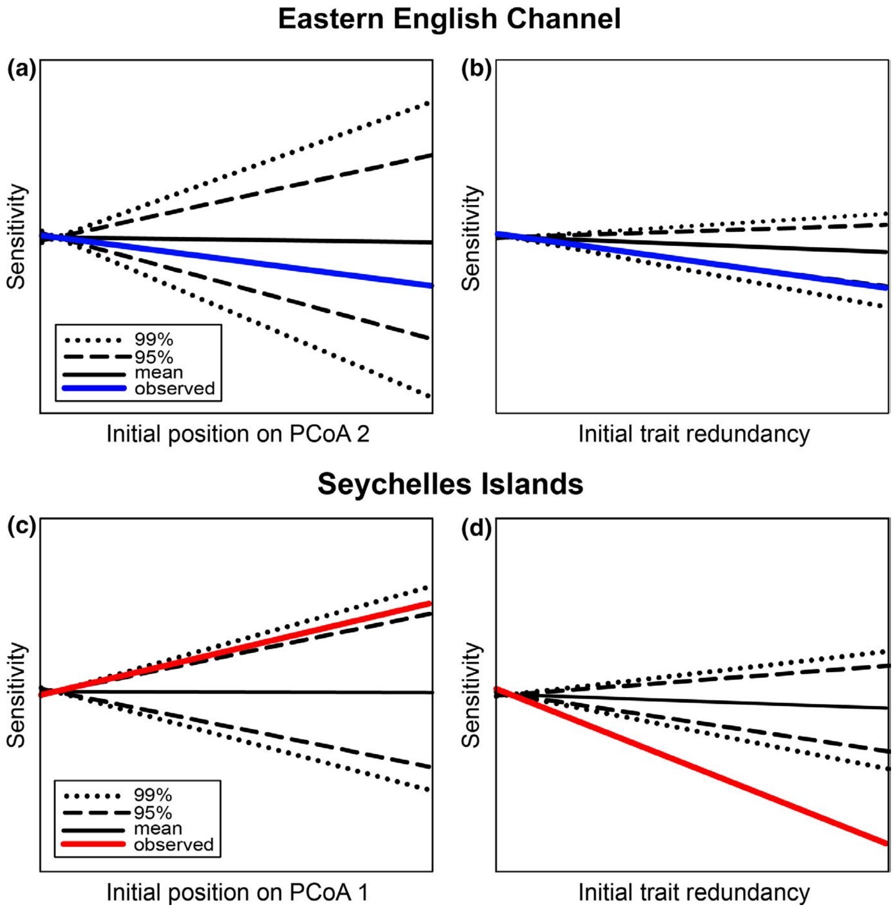
Eastern English Channel		Seychelles Islands	
Factors	AIC weight, mean ± *SD*	Factors	AIC weight, mean ± *SD*
Trait redundancy	0.99 ± 0.01	Initial PCoA 1 position	0.56 ± 0.21
Initial PCoA 2 position	0.98 ± 0.03	Trait redundancy	0.44 ± 0.21
Δ Salinity	0.84 ± 0.13	Δ Coral cover (%)	0.33 ± 0.12
Δ Sea surface temperature	0.40 ± 0.10	Depth	0.32 ± 0.10
Depth	0.36 ± 0.07	Initial PCoA 2 position	0.24 ± 0.14
Initial PCoA 1 position	0.28 ± 0.07	Species richness	0.21 ± 0.04
Species richness	0.24 ± 0.01	Δ Reef complexity (%)	0.19 ± 0.06
		Management status	0.18 ± 0.02

Null models indicated that the slope of the relationship between sensitivity and initial PCoA 2 position was larger than expected by chance, albeit not significantly, as the observed slope was smaller than the 95% most extreme expected values (Figure 4a). However, the slope of the relationship between sensitivity and initial trait redundancy was significantly larger than expected by chance, as the observed slope was greater than 95% of slopes in the null distribution (Figure 4b).

3.2 | Reef-fish community responses to coral bleaching

In the Seychelles, the first two axes of trait space captured 52% of overall variation in fish trait structure for the 129 species (Figure 2c), while the third and fourth axes explained an additional 22%. The first axis of trait space was primarily characterized by differences between species with large size and age at

FIGURE 4 Results of null models comparing the observed slopes of the relationships between sensitivity and (i) initial PCoA 2 position, and (ii) initial trait redundancy in the Eastern English Channel (a, b) and between sensitivity and (i) initial PCoA 1 position, and (ii) initial trait redundancy in the Seychelles Islands (c, d). Solid black lines indicate the mean slope of the null models, while dashed lines and dotted lines indicate the 95th and 99th percentiles of the null models, respectively [Colour figure can be viewed at wileyonlinelibrary.com]



maturity, high mobility, piscivorous diets, and solitary behavior (lower values) versus small, fast-growing planktivores and corallivores with high parental care (i.e., hide and guard eggs within coral habitats), and schooling behavior (higher values), while the second axis was characterized by differences between invertivore feeders with solitary behavior and closer association the benthos (lower values) versus piscivores and microphages with higher position in the water column (higher values; Figure 2b; Figure S3). We found that the distance moved by each community between the two time periods (1994 and 2005) was significantly correlated with the initial position of each community along PCoA axis 1, as communities with higher PCoA 1 scores had larger changes in trait structure ($r = 0.56$, $p < 0.01$; Figures 2d and 3d; Figure S1). We next found that the distance moved by each community was also significantly and negatively correlated with initial trait redundancy, as communities with higher trait redundancy were less sensitive and more resistant to changes in trait structure ($r = -0.59$, $p < 0.01$; Figure 3e). GLMs then ranked trait redundancy, PCoA 1 position, and coral cover change as the most important independent variables predicting the distance moved by each community in trait space (top 3 variables, Table 1) with secondary contributions by depth, PCoA 2 position, species richness, reef complexity change, and management status. Finally, Moran's *I* revealed that there was no spatial autocorrelation in the model residuals ($p = 0.49$).

Null models indicated that the slope of the relationship between sensitivity and both (a) initial PCoA 1 position and (b) initial trait redundancy were significantly larger than expected by chance, as the observed slopes were greater than 95% and 99% of slopes in the null distributions, respectively (Figure 4c,d).

4 | DISCUSSION

Despite wide belief that trait structure and redundancy can determine community sensitivity to disturbance, little evidence exists from natural systems over large temporal and spatial scales. Additionally, while functional ecology has operated on the presumed buffering capacity of trait redundancy, few studies have quantitatively demonstrated links between trait redundancy and community sensitivity outside of controlled experiments. Here, we present one of the first studies using long-term data in two distinct ecosystems showing that trait structure and redundancy may determine community sensitivity to disturbance and that trait redundancy may buffer communities against environmental change. Past experimental and small-scale observational studies have shown that higher levels of trait redundancy can maintain community stability in the face of environmental change (Allison & Martiny, 2008; Loreau, 2004; Rosenfeld, 2002; Wohl, Arora, & Gladstone, 2004); however, here we used datasets spanning nearly 25 years to examine changes in large, natural ecosystems in both temperate and tropical environments. Our findings support long-standing theory that higher diversity (i.e., richness and abundance) supporting ecological roles can generate greater community stability, reducing sensitivity to climatic disturbances (Elmqvist et al., 2003; Rosenfeld, 2002; Walker, 1992).

As disturbances in both ecosystems were related to climate warming, our results provide insight for understanding biodiversity responses to climate change. Not only were communities with lower trait redundancy more sensitive to climatic disturbances, but dominance by certain trait values rendered communities particularly sensitive to disturbance. For instance, in the EEC, dominance by small, r-selected pelagics led to greater shifts in trait structure through time as small pelagic species are highly responsive to environmental change, particularly warming and changes in oceanographic processes (Alheit et al., 2014; Lindegren, Checkley, Rouyer, MacCall, & Stenseth, 2013; Rijnsdorp et al., 2009). Pelagic fishes are also highly mobile and can quickly migrate or shift distribution, whereas demersal and reef-associated taxa may have greater site fidelity and less response capacity (Alheit et al., 2014; Lindegren et al., 2013; McLean et al., 2018; Rijnsdorp et al., 2009). In the Seychelles, communities more dominated by small, gregarious corallivores and planktivores were more impacted by large-scale coral mortality, which is consistent with studies showing that small-bodied fishes feeding on and around corals typically decline following disturbance (Graham et al., 2007; Pratchett et al., 2008; Richardson, Graham, Pratchett, Eurich, & Hoey, 2018). While the climatic vulnerability of small pelagics and small corallivores is well documented, our approach demonstrates that initial trait structure can predict community sensitivity to climatic disturbance, which is likely applicable across ecosystems and taxa. Our results therefore highlight the need to identify key trait–environment relationships in marine ecosystems worldwide to anticipate how climate warming might impact current and future communities through changes in trait structure.

While certain trait structures rendered communities more sensitive to disturbance, communities with higher trait redundancy were more resistant. Trait redundancy may buffer communities through multiple underlying mechanisms. According to the portfolio effect, if community structure is supported by many ecologically similar species and these species exhibit asynchronous responses to disturbance, the lesser impacted species should maintain overall community structure (Loreau & de Mazancourt, 2013; Oliver et al., 2015; Yachi & Loreau, 1999). High evenness, where each ecological role is supported by similar species richness and abundance, should also increase community resistance, whereas communities overrepresented by few, dominant species may leave some ecological roles with low redundancy and weak insurance (Flöder & Hillebrand, 2012; Oliver et al., 2015; Wittebolle et al., 2009). For instance, if evenness is low and dominant species are sensitive to disturbance, communities will be highly impacted, but if evenness is high, resistant species may maintain or recover community structure (Flöder & Hillebrand, 2012; Wittebolle et al., 2009). Additionally, redundancy in species interactions may buffer communities by increasing food web stability. For example, loss of key trophic interactions can destabilize community structure (Kuiper et al., 2015), and trophic redundancy has been shown to reduce vulnerability to cascades (Sanders et al., 2018). In the EEC, trait diversity was relatively similar across communities, while taxonomic diversity was higher along the coasts, leading to greater trait redundancy, as ecological roles were supported by more species and greater abundances (Figure S6). Communities exhibiting the greatest shifts in trait structure had low species richness and abundance, meaning some ecological roles had only limited support. Although pelagic fishes were highly impacted throughout the ecosystem, resistant communities had higher richness and abundance of pelagics, which appeared to buffer them against changes in trait structure. For example, horse mackerel exhibited exceptional declines (Auber et al., 2015, 2017) and communities mainly dominated by horse mackerel suffered major shifts from pelagic to demersal structure, whereas communities with large abundances of not only horse mackerel but also sprat, herring, and Atlantic mackerel (ecologically similar species) had greater capacity to maintain initial structure (Figure 5). It therefore appears that the combination of higher richness and evenness supporting similar levels of trait diversity in the EEC leads to higher resistance and lower sensitivity.

It is also important to note that higher trait diversity does not necessarily correspond to higher overall trait redundancy, as ecologically simple communities can have high redundancy (Casatti et al., 2015; Fonseca & Ganade, 2001; Mouillot et al., 2014). In the Seychelles, the most impacted communities were actually those with the highest trait diversity—species in these communities varied greatly in trait composition. However, taxonomic diversity was more similar among communities, indicating that, although impacted communities had high trait diversity, individual ecological roles were supported by fewer species and individuals (Figure S7). Thus, higher trait redundancy in resistant communities resulted from similar levels of richness and abundance being shared among fewer ecological roles. Additionally, it is important to note that the impact of ecological disturbances and the buffering capacity of trait redundancy depend on the type of disturbance and on which ecological roles are affected. For instance, the least impacted communities in the Seychelles were intuitively those with lower abundances of small corallivores. Thus, while the ecological roles supported by these species, for example, shaping coral diversity (Cole, Pratchett, & Jones, 2008), were most impacted following disturbance, these roles were already low in unaffected communities. Hence, unaffected communities had high trait redundancy within ecological roles (e.g., large-bodied invertivores) that were not heavily impacted by disturbance. Yet, if the impacted ecological roles had been highly redundant, sensitive communities may have been more resistant. For instance, communities more characterized by small-bodied, site-attached corallivores and planktivores had higher sensitivity. However, corallivores and planktivores accounted for only 12% of all species and only 14% of trophic guild abundance on average, whereas invertivores accounted for 43% of species and 46% of trophic guild abundance. Thus, if small-bodied corallivores and planktivores had greater initial redundancy, sensitive communities may have been buffered against disturbance,

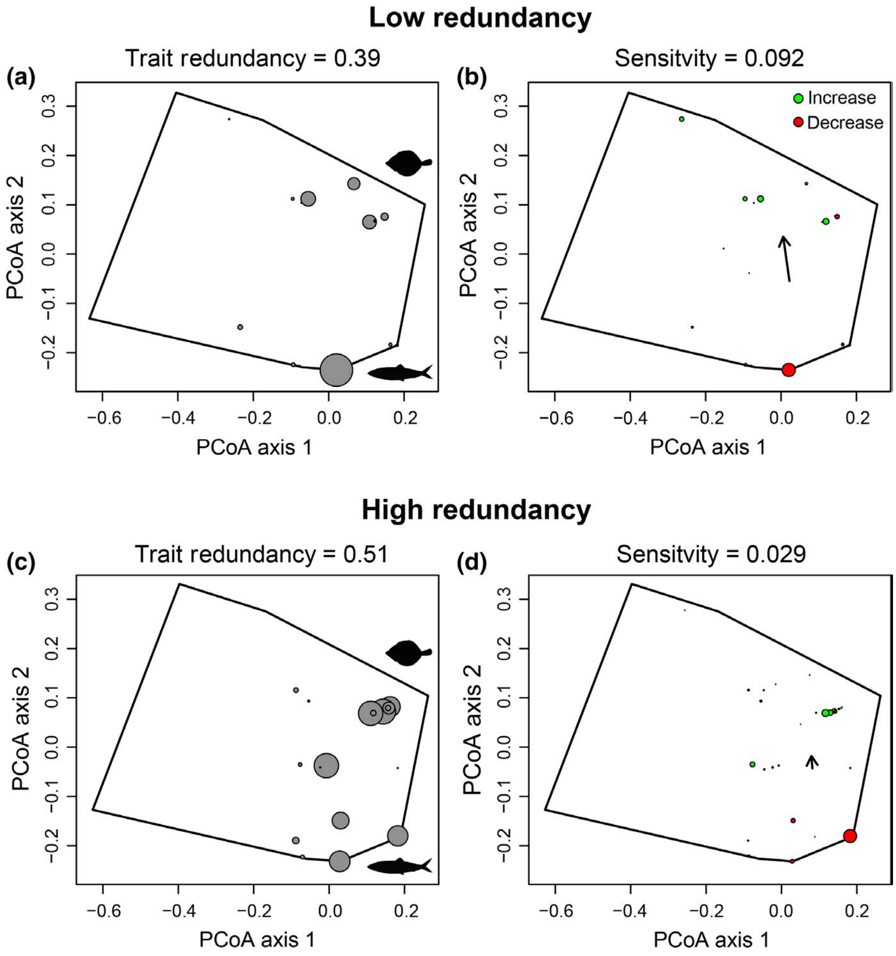


FIGURE 5 Relationship between trait redundancy and sensitivity in two fish communities from the Eastern English Channel (chosen to highlight low and high redundancy examples). In panels a and c, circles represent species, and circle sizes are scaled by initial (i.e., predisturbance) abundances. In panels b and d, circle sizes are scaled by species' abundance changes and colors indicate whether abundances increased or decreased. The community with low trait redundancy (a, b) had only one dominant species supporting the pelagic ecological role (bottom-right corner), while the community with high trait redundancy (c, d) had multiple abundant species supporting the pelagic role. Both sites suffered major declines in one pelagic species and minor increases in demersal species (b, d). However, the site with low trait redundancy underwent a major shift from pelagic to demersal community structure (b), whereas the site with high trait redundancy was resistant to change (d), as the remaining abundant pelagic fishes maintained the ecological role [Colour figure can be viewed at wileyonlinelibrary.com]

particularly through additional species with asynchronous environmental responses.

While our findings support the conclusion that trait redundancy may buffer communities against disturbance, alternative explanations are possible. For example, trait structure and redundancy are intrinsically correlated with environmental conditions, and we found that sensitivity was also related to environmental change in both ecosystems. In the EEC, salinity changes may have contributed to declines in species with small pelagic eggs and larvae, as salinity influences egg buoyancy and survival (Nissling, Nyberg, & Petereit, 2017; Petereit et al., 2009; Sundby & Kristiansen, 2015). However, salinity changes in the EEC were much lower than those normally reported to impact fish community structure (Petereit et al., 2009; Sirot et al., 2015). In the Seychelles, we found that fish communities experiencing greater losses of coral cover and at shallower depths had higher sensitivity and lower resistance to disturbance, which is in line with previous studies showing that coral loss reorganizes reef fish communities (Richardson et al., 2018) and that shallower communities are more sensitive to disturbances such as bleaching (Bridge et al., 2013). If sensitivity in the Seychelles was driven by greater environmental impacts, the apparent buffering capacity of trait redundancy could be an artifact of lower redundancy on reefs with greater coral loss. However, it is likely that both initial biological structure and local environmental changes are driving sensitivity and their influences may be synergistic.

As with all trait-based approaches, the choice and number of traits may have important impacts on the patterns of trait diversity and redundancy (Lepš, de Bello, Lavorel, & Berman, 2006; Violle & Jiang, 2009; Violle et al., 2007). For example, communities may have little redundancy along one niche axis, but high redundancy along another, and contrasting trends in the two axes could blur redundancy patterns (Micheli & Halpern, 2005; Spasojevic & Suding, 2012). However, multiple traits are needed to capture nuances among species, as combinations of traits (e.g., habitat type and life history) may act synergistically, leading to higher or lower disturbance sensitivity (Mouillot et al., 2013; Villéger et al., 2017; Villéger, Miranda, Hernández, & Mouillot, 2010). However, re-running our analyses with all combinations of six out of seven traits did not substantially modify results, as trait structure and redundancy emerged as the most important explanatory factors of sensitivity (Figures S4 and S5).

While we examined the influence of biological structure on community sensitivity to disturbance, future studies should also examine the environmental drivers of trait redundancy itself. Linking gradients in environmental condition or human stressors to trait redundancy could be particularly informative for resource management. If human stressors are reducing trait redundancy, management strategies could be adapted to enhance redundancy for increased resilience against future disturbances. In the

Seychelles Islands, management status was not linked to environmental sensitivity, yet other natural and human drivers such as productivity or watershed pollution could have shaped initial trait structure and redundancy. While we were unable to quantify the influence of historical fishing pressure on sensitivity in the English Channel, past studies have concluded that overfishing may have rendered fish communities more sensitive to climatic changes by removing large demersal predators (McLean et al., 2018; Molfese, Beare, & Hall-Spencer, 2014). Thus, identifying the natural and anthropogenic drivers of ecological-trait structure and redundancy should be prioritized in future studies and resilience assessments. Future studies should also attempt to identify thresholds of ecological trait and trait redundancy values to reveal tipping points in ecosystem stability that could be used as tangible management targets for maintaining resilience. As biodiversity loss threatens ecosystem functioning worldwide, identifying and conserving the mechanisms of community stability will be critical to maintaining the diversity needed to support ecosystem services.

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