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

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ABSTRACT – 150 word limit for Ecology Letters

Functional diversity is predicted to influence ecosystem dynamics through links between organismal traits and ecosystem processes. Theory predicts that key functional traits and high functional redundancy can buffer communities against environmental disturbances. While experimental evidence and data from simple ecological systems support these notions, evidence from natural experiments with large species assemblages is lacking. Using long-term data from both temperate and tropical fish assemblages, we examine how initial functional-trait structure and functional redundancy buffer communities against ecological shifts during disturbance. We find that functional vulnerability to disturbance increases depending on both initial functional-trait structure and lower functional redundancy of communities. In both temperate and tropical fish assemblages, increasing dominance by climatically-sensitive functional traits rendered communities more susceptible to ecological shifts, while communities with higher functional redundancy were more resistant to change. Our results exemplify a consistent link between biological structure and ecosystem vulnerability, providing insight for anticipating future disturbance impacts on biodiversity.

INTRODUCTION

Global environmental change threatens the stability of ecosystem functions and services, with severe consequences, such as food insecurity, predicted by the end of the century (Bellard *et al.* 2012; IPCC 2014; Melillo 2014). Accordingly, understanding how variation in biodiversity influences the vulnerability of communities and ecosystems to environmental change is crucial (Bellard *et al.* 2014; Beaugrand *et al.* 2015; Segan *et al.* 2016; Heilpern *et al.* 2018). Species

42   diversity has been shown to enhance ecosystem productivity and to buffer communities against

43   environmental disturbances (Worm *et al.* 2006; Naeem *et al.* 2012; Mellin *et al.* 2014; Schneider

44   *et al.* 2016). A functional approach enables exploration of the impacts of biodiversity loss on

45   ecosystem processes and services (Sakschewski *et al.* 2016; Soliveres *et al.* 2016; Gross *et al.*

46   2017). Functional diversity measures are used to describe ecosystem functioning, as organismal

47   traits can be linked to ecosystem processes like nutrient cycling and biomass production, and can

48   provide a mechanistic understanding of community changes via trait-environment relationships

49   (Bejarano *et al.* 2017; Cadotte 2017; Henriques *et al.* 2017; Villéger *et al.* 2017).

50   The presence of key ecological functions (i.e., functional traits or groups) and high functional

51   redundancy can buffer communities against the impacts of environmental change (Díaz & Cabido

52   2001; Laliberte *et al.* 2010; Dee *et al.* 2016; Nash *et al.* 2016; Sanders *et al.* 2018). For instance,

53   on coral reefs key functions such as grazing and bio-erosion by large parrotfishes maintain benthic

54   community structure following disturbances (Bozec *et al.* 2016; Heenan *et al.* 2016; McLean *et al.*

55   2016), and high diversity within parrotfish groups can reinforce these functions (Walker 1992;

56   Burkepile & Hay 2008; Sanders *et al.* 2018). However, functional redundancy may not always

57   buffer communities, particularly when functionally synonymous species exhibit similar negative

58   responses (i.e., low response diversity) (Laliberte *et al.* 2010), and long-term empirical evidence

59   demonstrating the buffering effects of functional redundancy is lacking.

60   While community responses are normally linked directly to environmental variation,

61   environmental gradients ultimately lead to variability in community structure, which can determine

62   biological responses to disturbance (McIntyre *et al.* 1995; Chapin *et al.* 1997; Fukami *et al.* 2005;

63   Williams *et al.* 2010). Therefore, when examining why some communities are vulnerable to

64   disturbances while others are resistant, it is necessary to address biological variability among

65   communities. Two potential biological mechanisms may explain differences in vulnerability

66   among neighboring communities: 1) communities differ in biological composition such that some

67   communities are more dominated by species with vulnerable (or resistant) functional traits, and

68   community structure is more weighted by these traits (McLean et al. MEPS), or 2) vulnerable

69   communities have lower levels of functional redundancy (Walker 1992; Williams *et al.* 2010).

70   Thus communities' initial functional composition and diversity at a baseline time period (i.e., pre-

71   disturbance) could determine communities' vulnerability or resistance to environmental

72   disturbances.

73   Here, using multidimensional functional spaces based on species' functional traits, we show

74   how the vulnerability of communities' functional structures is determined both by initial

75   functional-trait composition and by initial functional redundancy. Using long-term data from both

76   north-temperate and tropical-reef fish assemblages, we show that increased dominance by

77   climatically-sensitive functional traits rendered communities more susceptible to ecological shifts,

78   while communities with higher functional redundancy were more resistant to change.

79

80   **MATERIALS AND METHODS**

81   **Eastern English Channel: temperate marine fish communities**

82   **Disturbance**

83   The fish assemblage of the Eastern English Channel (EEC) experienced a major shift in both

84   taxonomic and functional structure in the late 1990s in response to an Atlantic-wide climate

85   oscillation (The Atlantic Multidecadal Oscillation) that led to rapid sea surface warming and

86   oceanographic changes (Ting *et al.* 2009; Auber *et al.* 2015, 2017 McLean et al. MEPS). While all

87   sampling sites throughout the EEC were concurrently impacted by a basin-wide climate

88   disturbance, the amplitude of community change was highly variable among sites, with some sites

89   experiencing very pronounced shifts and others remaining relatively unchanged (Auber *et al.* 2017)

90   (McLean et al. MEPS).

91

Fish community data

92

93   The fish community of the EEC (area VIId defined by the International Council for the Exploration

94   of the Sea, ICES) has been sampled every October since 1988 during the Channel Ground Fish

95   Survey (CGFS). Here, we focused on the study period of 1988 – 2011. The CGFS sampling scheme

96   is spatially stratified by subdividing the EEC into 15'×15' rectangles where at least one 30-min

97   haul is made during daylight hours at an average speed of 3.5 knots. A high (3 m) vertical opening

98   bottom trawl (GOV) with a 10-mm-stretched-mesh-size codend was used. The stratified sampling

99   scheme completed 90 to 120 hauls per year depending on weather conditions. After each haul, all

100   captured fishes were identified and counted. Abundance indices at each sampling station were

101   obtained from the ICES data portal and were standardized to numbers of individuals per km^2

102   (ICES). Abundance data were $log_{10}(x+1)$ transformed before analyses.

103

Functional traits

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105   Nine functional traits related to life history, habitat use, and trophic ecology were collected for 73

106   taxa (67 species, 6 identified to genera only). These included length and age at maturity, fecundity,

107   offspring size, water column position, temperature preference, trophic guild, and trophic level.

108   Temperature preference was calculated as the median temperature of a species across its global

109   range of observations for which data were available. Trait data came from FishBase (Froese &

110   Pauly 2012), the Ocean Biogeographic Information System (http://www.iobis.org/), the Global

111   Biodiversity Information Facility (https://www.gbif.org/), Engelhard *et al.* (2011), and Pecuchet *et*

112   *al.* (2017). Functional traits were chosen if they were potentially implicated in community

113   responses to environmental change (McLean et al. MEPS) and based on sufficient availability and

114   accuracy.

115

116   **Environmental factors**

117   Environmental parameters included depth, sea surface temperature (SST), salinity, and

118   chlorophyll-*a*, which were all collected *in-situ* at each survey site during the CGFS monitoring

119   campaigns. However, spatially-resolved data for chlorophyll-*a* were not available prior to 1998.

120

121   **Seychelles Islands: coral reef-fish communities**

122   **Disturbance**

123   The Seychelles Islands experienced wide-spread coral mortality following severe coral bleaching

124   during the 1998 El Niño, which led to substantial changes in reef fish taxonomic and functional

125   structure (Graham *et al.* 2006, 2015). The mass bleaching was severe across the entire inner

126   Seychelles (Graham *et al.* 2006, 2015), and of the 21 sites surveyed, all but one site had losses in

127   coral cover, with an average 65% loss across all sites. While differential benthic trajectories

128 following the mass bleaching have been linked to environmental and ecological conditions

129 (Graham *et al.* 2015), variation in initial disturbance vulnerability has not yet been investigated.

130

131 **Fish community data**

132 Fish abundance data were collected at 21 sites around the Seychelles Islands using underwater

133 visual census (UVC) in both 1994 (pre-disturbance) and 2005 (post-disturbance). At each site 16

134 individual 7-m radius (154m-2) stationary point counts were surveyed along the reef slope, and the

135 identity, density and individual sizes of diurnally active, non-cryptic reef fishes were recorded

136 within each count (Graham *et al.* 2006, 2015). Abundance data were $\log_{10}(x+1)$ transformed before

137 analyses.

138

139 **Functional traits**

140 Four functional traits related to habitat use, behavior, and trophic ecology were collected for the

141 129 species sampled. Trait data came from both FishBase (Froese & Pauly 2012) and previously

142 published literature (WILSON S. K. *et al.* 2008; Graham *et al.* 2011; Stuart-Smith *et al.* 2013;

143 Graham *et al.* 2015). These included maximum length, diet, gregariousness, and habitat

144 specialization (i.e., facultative vs. obligate relation with corals). Functional traits were again chosen

145 because they have been implicated in the response of coral reef fish communities to environmental

146 change (Wilson et al. 2006 GCB; Pratchett et al. 2008 OMBAR, Graham et al. 2011 Ecol Lett).

147

148 **Environmental factors**

149 Environmental data included depth, coral cover, reef complexity, and management status (i.e.,

150 fished vs. marine reserve). Within each stationary point count, the percent cover of live hard coral

151 was quantified and the structural complexity of the reef were visually estimated (Graham *et al.*

152 2006, 2015). Structural complexity was assigned to one of the five categories: 0 = no vertical relief,

153 1 = low (<30 cm) and sparse relief, 2 = low but widespread relief, 3 = widespread moderately

154 complex (30–60 cm) relief, 4 = widespread very complex (60–100 cm), and 5 = exceptionally

155 complex (>1 m) relief, which aligns with several other methods of assessing structural complexity

156 on coral reefs (Graham *et al.* 2006, 2015).

157

158 **Quantifying functional vulnerability**

159 **Multidimensional functional space**

160 We created a functional-trait space for each ecosystem where species are arranged according to

161 their functional trait composition, and species' relative positions are based on their functional

162 similarity (Villéger *et al.* 2008; Laliberté & Legendre 2010; Mouillot *et al.* 2013). We created

163 functional-trait space by first creating a Gower dissimilarity matrix of the species by trait table,

164 with species in rows and functional traits in columns. Gower dissimilarity is well-adapted for

165 examining functional traits as it can handle multiple data types (i.e., continuous and categorical)

166 and missing values (Gower 1971; Laliberté & Legendre 2010). Functional space was then built by

167 ordinating the Gower similarity matrix using principal coordinates analysis (PCoA) (Mouillot *et*

168 *al.* 2013).

169

170   **Functional vulnerability**

171   We quantified 'functional vulnerability' as the amplitude of change in functional-trait structure

172   before and after disturbance using the functional-trait space. Large shifts in functional structure

173   indicate low resistance and thus high vulnerability, while small shifts indicate high resistance and

174   low vulnerability. For a given ecosystem, we first calculated abundance-weighted community

175   centroids on the first two axes of functional space for all sites in all time periods (Fig. 1a). Within

176   the functional-trait space, the location of any given site in any given year is defined as the centroid

177   of all species for that site, weighted by species' abundances (Fig. 1a). Thus, the movement of a site

178   in the functional-trait space can be used to quantify changes in functional-trait structure through

179   time. We therefore calculated functional vulnerability as the distance between a site's position in

180   functional space before and after a disturbance (Fig. 1b). This quantifies the amount of distance

181   each site moved in functional space during a disturbance, where sites with larger movements

182   display higher vulnerability and sites with smaller movements display higher resistance.

183   Additionally in the case of long time series that exhibit gradual changes (i.e., no abrupt phase

184   change or regime shift), it is possible to quantify vulnerability as the absolute value of the slope of

185   the movement of a site or community along the functional space axes. Sites with large changes in

186   functional structure through time (i.e., high vulnerability) will have large slopes along either one

187   or both axes of functional space. In the case of EEC, where an abrupt community shift occurred in

188   the middle of a long time series, for each site, we calculated the distance between the average

189   positon of all years before and all years after the disturbance, while in the Seychelles, for each site,

190   we calculated the distance between 1994 (pre-bleaching) and 2005 (post-bleaching).

191

192
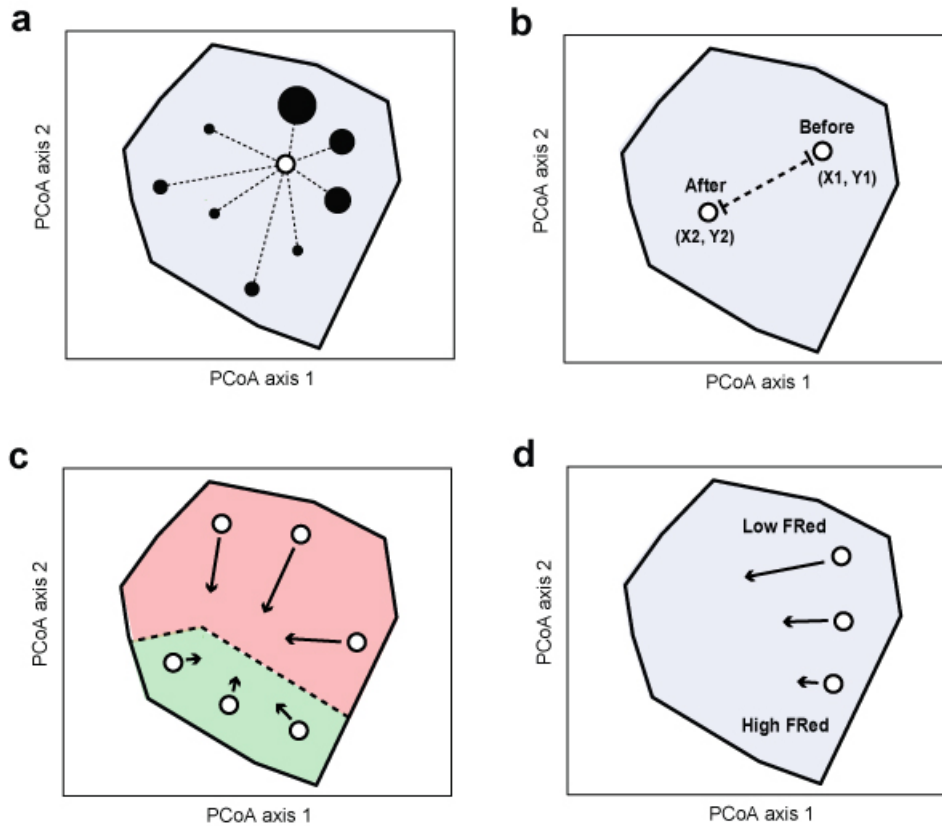
Figure 1. Conceptual diagrams showing the calculation of functional vulnerability according to change in the abundance-weighted community position of a site (a) before and after disturbance (b), along with potential links between functional vulnerability and i) functional-trait structure (c) and ii) functional redundancy (FRed) (d).

Functional Redundancy

Functional redundancy quantifies the degree to which species in a community share similar functional characteristics, i.e., whether functional strategies are supported by few or many species. Here, we quantified functional redundancy following de Bello *et al.* (2007), where functional redundancy is parsimoniously defined as the degree to which a community is 'saturated' with similar functional traits, and is calculated as the difference between taxonomic diversity (Simpson's index) and functional diversity (Rao's quadratic entropy) (de Bello *et al.* 2007). In this

205   fashion, communities with the same level of functional diversity but different levels of species

206   richness (or vice versa) will vary in functional redundancy, where a community with either more

207   functionally similar species or higher species richness will have higher functional redundancy.

208   Previous studies quantifying functional redundancy using this metric found significant

209   relationships with community stability and environmental filtering (Pillar *et al.* 2013; Kang *et al.*

210   2015; Bruno *et al.* 2016). Additionally, this metric of functional redundancy is calculated at the

211   community level using continuous data, and does not require defining functional groups, which

212   can be subjective and controversial. Initial functional redundancy (i.e., pre-disturbance) was

213   calculated for all sites in both ecosystems using the R package *SYNCSA*.

214

Generalized Linear Models (GLM)

216   When considering the influences of environmental variables, we calculated the change in each

217   variable before and after disturbance for each site rather than using temporally-averaged spatial

218   variables to avoid using static independent variables to predict dynamic dependent variables. Thus,

219   changes in local environmental parameters were used to predict changes in functional-trait

220   structure. For instance, while the EEC was impacted by an Atlantic-wide climate oscillation and

221   associated ocean warming, local-scale variability in SST or salinity change could explain

222   variability in community responses. Depth was the only parameter included in all statistical models,

223   as it is a permanent environmental condition (on ecological time scales). Therefore, in the EEC,

224   we built general linear models (GLMs) testing the influences of i) the initial position of each site

225   in functional-trait space (PCoA 1 and PCoA 2 scores), ii) the initial functional redundancy, iii)

226   species richness, iv) depth, v) changes in local SST, and vi) changes in local salinity on the

227   functional vulnerability of each site.

228   In the Seychelles, we used GLMs to test the influences of i) the initial position of each site

229   in functional space (PCoA1 and PCoA2 scores), ii) the initial functional redundancy, iii) species

230   richness, iv) depth, v) percent change in coral cover, vi) percent change in reef structural

231   complexity, and vii) management status on functional vulnerability. All GLM models were

232   assessed using Akaike weights to identify the most contributive independent variables, and the R

233   package *visreg* was used to examine relationships between independent and dependent variables

234   while accounting for co-variation among independent variables.

235

236   **Null Models**

237   To examine whether the relationships between functional vulnerability and i) initial functional-trait

238   structure, or ii) initial functional redundancy were significantly different than expected by random

239   chance, we built null models examining the slope of the linear regression between functional

240   vulnerability and each metric, following Fukami *et al.* (2005). For each null model we randomly

241   permutated the species by abundance table, re-calculated abundance-weighted community

242   centroids in functional space, re-calculated functional redundancy, and re-computed the

243   corresponding linear models. This process was repeated 1000 times and the corresponding linear

244   modes were used to build null distributions of 1000 slopes. The actual observed slopes between

245   functional vulnerability and i) initial position in functional space, and ii) initial functional

246   redundancy were then compared to the resulting null distributions.

247

RESULTS

Climatic disturbance in a temperate marine fish community

In the EEC, the first two axes of functional-trait space captured 48% of overall variation in functional structure among the 73 taxa (Fig. 2a). The first axis of functional space was primarily characterized by differences between large-bodied, long-lived, high trophic-level species with large offspring size (higher values) vs. small-bodied, short-lived pelagic species, and detritivores (lower values), while the second axis was characterized by differences between carcinophages and benthopiscivores with high parental care (higher values) vs. pelagic and mesopelagic species and planktivores and detritivores (lower values) (Fig. 2a). We found that the distance each site moved in functional space before and after the disturbance (1997), was significantly correlated to the initial position of each site along the second axis of the functional space, as sites with lower PCoA 2 values had higher changes in functional-trait structure before and after the disturbance ($r = -0.28$, $P = 0.01$). We next examined whether the distance moved in functional space was related to initial values of functional redundancy (mean functional redundancy across all years prior the regime shift). We found that distance moved was significantly and negatively correlated to functional redundancy: sites with higher functional redundancy were more resistance and had less pronounced shifts ($r = -0.46$, $P < 0.0001$). GLM models then ranked functional redundancy, initial PCoA 2 position, depth, and local changes in salinity as the most important independent variables predicting the distance moved by each site in functional-trait space (Fig. 2b-d, Fig. S1, Fig. S2). Distance moved (i.e., functional vulnerability) was higher in deeper sites and in sites where salinity decreased before and after the disturbance (Fig. S1, Fig. S2).
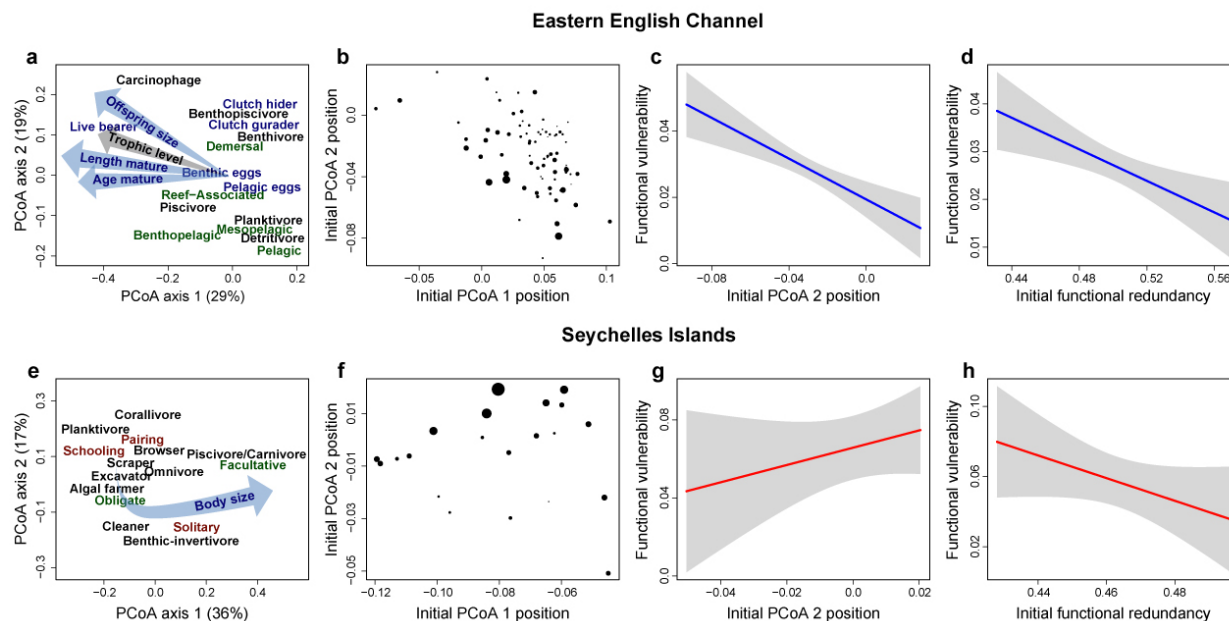
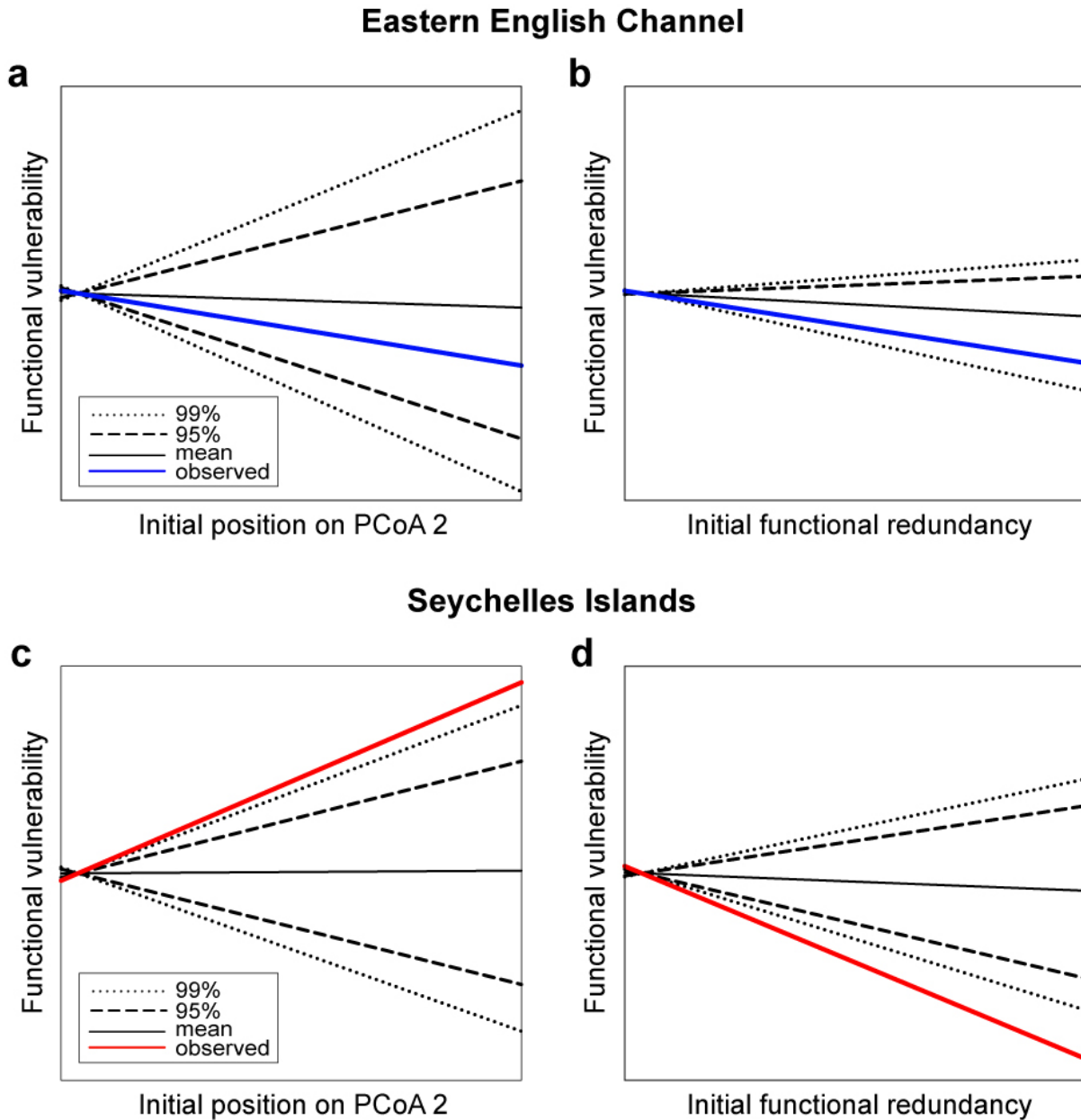**Figure 2.** Relationships between functional vulnerability and the initial functional structure of communities in the Eastern English Channel (EEC) and Seychelles Islands. a) Functional-trait structure of the overall fish community of the EEC. b) Functional vulnerability of each site in the EEC defined by the distance moved (i.e., amplitude of change) along the first two axes of functional-trait space before and after disturbance; larger circles = higher movement and therefore higher vulnerability. Relationships between functional vulnerability and c) initial position on PCoA axis 2 of functional-trait space, and d) initial functional redundancy in the EEC. e) Functional-trait structure of the overall fish community of the Seychelles. f) Functional vulnerability of each site in the Seychelles. Relationships between functional vulnerability and g) initial position on PCoA axis 2 of functional-trait space, and h) initial functional redundancy in the Seychelles.

Null models indicated that the slope of the relationship between functional vulnerability and initial PCoA 2 position was larger than expected by random chance, but not significantly so, as the observed slope was smaller than the 95% most extreme expected values (Fig 3a). However, the slope of the relationship between functional vulnerability and initial functional redundancy was significantly larger than expected by random chance, as the observed slope was greater than 95% of slopes in the null distribution (Fig 3b).

Eastern English Channel

Seychelles Islands

Figure 3. Results of null models comparing the observed slope of the relationship between functional vulnerability and i) initial position on the second axis of functional-trait space, and ii) initial functional redundancy in the Eastern English Channel (a, b) and Seychelles Islands (c, d).

Reef-fish community responses to coral bleaching

295   In the Seychelles, the first two axes of functional-trait space captured 54% of overall variation in

296   functional structure among the 129 species (Fig. 2e). The first axis of functional space was

297   primarily characterized by differences between large-bodied species, facultative species, and

298   piscivores/carnivores (higher values) vs. planktivores, schooling species, scraping herbivores, and

299   algal farmers (lower values), while the second axis was characterized by differences between

300   corallivores, planktivores, pairing, and schooling species (higher values) vs. benthic invertivores,

301   solitary species, and larger-bodied species (lower values) (Fig. 2e). We found that the distance

302   moved by each site between the two time periods (1994 and 2005) was significantly correlated to

303   the initial position of each site along PCoA axis 2, as sites with higher PCoA 2 scores had larger

304   changes in functional-trait structure ($r = -0.60$, $P = 0.004$). We next found that the distance moved

305   by each site was also significantly and negatively correlated to the initial functional redundancy of

306   each site, as sites with higher functional redundancy were less vulnerable and more resistant to

307   changes in functional-trait structure ($r = -0.55$, $P = 0.009$). GLM models then ranked depth,

308   functional redundancy, initial PCoA 2 position, and management status as the most important

309   independent variables predicting the distance moved by each site in functional-trait space (Fig. 2f-

310   h, Fig. S1, Fig. S2). Distance moved (i.e., functional vulnerability) was higher in shallower sites

311   and in openly fished sites (Fig. S1, Fig. S2).

312   Null models indicated that the slope of the relationship between functional vulnerability

313   and both i) initial PCoA 2 position and ii) initial functional redundancy were significantly larger

314   than expected by random chance, as the observed slopes were greater than 99% of slopes in the

315   null distributions (Fig 3c,d).

316

DISCUSSION

To our knowledge, ours is the first extensive study using long-term data to show that functional redundancy can buffer change in the functional structure of large species assemblages against environmental disturbances. Past experimental studies and studies from simple ecological systems have shown that higher levels of functional redundancy can maintain community stability in the face of environmental change (Rosenfeld Jordan S. 2002; Loreau Michel 2004; Allison & Martiny 2008). However, here we use datasets spanning nearly 25 years to examine changes in large natural ecosystems in both temperate and tropical environments. Our findings support long-standing ecological theory that a higher proportion of species supporting similar ecological functions can generate greater community stability, reducing vulnerability to climatic disturbances (Walker 1992; Rosenfeld Jordan S. 2002; Elmqvist *et al.* 2003).

As disturbances in both ecosystems were related to climate warming, our results provide critical information for future conservation planning and ecosystem management under climate change. Not only were communities with lower functional redundancy more vulnerable to climate-based disturbances, but dominance by certain functional traits rendered communities particularly sensitive to disturbance. For example, in the EEC increasing dominance by small pelagics led to greater shifts in functional structure through time as small pelagic species are highly impacted by ocean warming and changes in oceanographic processes (Rijnsdorp *et al.* 2009; Lindegren *et al.* 2013; Alheit *et al.* 2014). In the Seychelles, communities more dominated by small, schooling corallivores and planktivores were more impacted by large-scale coral mortality (Graham *et al.* 2007; Pratchett *et al.* 2008; Richardson *et al.* 2018). Interestingly, in both ecosystems, small, quickly reproducing species were most impacted by climatic disturbances. This is an interesting result as fishing down the food web in marine ecosystems generally removes large, long-lived

340   species first, leading to communities dominated by smaller, shorter lived species. Thus global

341   overfishing is likely leading to fish communities dominated by species with climatically sensitive

342   functional traits with reduced functional redundancy (McLean et al. MEPS) (Jackson *et al.* 2001;

343   Micheli & Halpern 2005; Pinsky & Byler 2015). This is alarming as historical human impacts have

344   likely rendered communities less resilient to the anticipated future impacts of climate change

345   (Graham *et al.* 2011). Our results highlight the need to identify trait-environment relationships in

346   marine ecosystems worldwide in order to anticipate how climate warming might impact current

347   and future communities through changes in functional-trait composition.

348   Beyond biological composition, both depth and salinity change influenced functional

349   vulnerability in the EEC, while depth and management status influenced vulnerability in the

350   Seychelles. In the EEC, sites where salinity decreased before and after the disturbance had greater

351   shifts in functional structure, as decreasing salinity levels can destabilize communities

352   (Wurtsbaugh & Berry 1990). Decreasing salinity may have driven declines in the abundance and

353   richness of species with narrow salinity tolerances, resulting in communities more dominated by

354   euryhaline species (Lappalainen Antti *et al.* 2000; Maes J. *et al.* 2005). Communities in shallower

355   depths were more resistant to change, while deeper communities were more vulnerable, exhibiting

356   greater ecological shifts. In the EEC, productivity (chlorophyll-*a*) is highest in shallow areas along

357   the coast, leading to higher species richness, greater abundance, and more functional redundancy

358   (Gentilhomme & Lizon 1997; Grioche *et al.* 1999). While it was not possible to calculate change

359   in chlorophyll-*a* before and after the disturbance, we did indeed find that temporally-averaged

360   chlorophyll-*a* values were strongly correlated to initial functional redundancy (McLean unpubl

361   data). In the Seychelles, we found that openly fished sites had greater shifts in functional structure

362   than marine reserves. Overfishing coral reefs has been shown to reduce ecological resilience and

363 increase vulnerability through reductions in both taxonomic and functional diversity, as fishing

364 quickly erodes key ecological functions (Jackson *et al.* 2001; Bellwood David R. *et al.* 2003; Houk

365 *et al.* 2017). In contrast to the EEC, communities in shallower depths had higher vulnerability and

366 lower resistance in the Seychelles. This is in line with previous studies showing that shallower

367 coral reef communities are more vulnerable to disturbances like bleaching (i.e., greater light

368 penetration and lower thermal inertia) and storm impacts (Bridge *et al.* 2013), and that deeper sites

369 have greater recovery potential (Graham *et al.* 2015).

370   Interestingly, higher functional redundancy does not necessarily correspond to higher

371 overall functional diversity, as functionally simple communities can have high functional

372 redundancy (Fonseca & Ganade 2001; Mouillot *et al.* 2014; Casatti *et al.* 2015). In the Seychelles,

373 the most impacted sites were actually those with the highest functional diversity, as species in those

374 communities varied greatly in functional-trait composition. However, species richness was similar

375 among all sites, suggesting that, although impacted sites were functionally diverse, individual

376 ecological functions were supported by few species. Additionally it is important to note that the

377 impact of ecological disturbances and the buffering capacity of functional redundancy are entirely

378 dependent on the type of disturbance and which ecological functions are affected. For instance, the

379 least impacted sites in the Seychelles were sites with the lowest levels of small, corallivorous

380 species. Thus while the functions provided by these species (e.g., shaping coral diversity [Cole

381 Andrew J. *et al.* 2008]) were most impacted, these functions were already low or absent in

382 unaffected sites. However, if the unaffected sites with high functional redundancy have low

383 response diversity (all species respond similarly to a given disturbance), a future disturbance could

384 drastically impact those communities (Laliberte *et al.* 2010; Bhaskar *et al.* 2018).

385   As with all functional-trait studies, the choice and number of functional traits have major

386   impacts on the calculation of functional diversity and redundancy (Leps *et al.* 2006; Violle *et al.*

387   2007; Violle & Jiang 2009). For example, communities may have little redundancy along one niche

388   axes, but high redundancy along another, and contrasting trends in the two axes could mask

389   redundancy patterns (Spasojevic Marko J. & Suding Katharine N. 2012). However, multiple

390   functional traits are needed to capture nuances among diverse species assemblages, as

391   combinations of traits (e.g., habitat type and life history) may act synergistically, leading to higher

392   or lower disturbance vulnerability (Villéger *et al.* 2010; Mouillot *et al.* 2013; Villéger *et al.* 2017).

393   We further advocate examination of functional structure and redundancy of large species

394   assemblages using long time series across ecosystems, species diversity gradients, and spatial

395   scales.

396

Conclusion

398   Despite wide belief that functional redundancy can buffer communities against the impacts of

399   environmental change, few studies have provided empirical support in large, natural ecosystems.

400   Here we found that communities dominated by particular functional traits and communities with

401   low functional redundancy were more impacted by environmental disturbances, providing strong

402   evidence for long standing ecological theories. Future studies should examine the influence of

403   functional structure and redundancy on ecological shifts using a variety of methods. Here, by using

404   functional-trait space, we directly examined changes in functional trait structure, but additional

405   methods for quantifying both taxonomic and functional vulnerability are possible. Future studies

406   should also attempt to identify thresholds of functional trait and functional redundancy values to

407   identify tipping points in ecosystem stability. Additionally, future research should examine the

408   influence of redundancy on community structure not only before and after disturbances, but during

409   recovery trajectories (Mouillot *et al.* 2013; Graham *et al.* 2015; Nash *et al.* 2016). While not

410   examined here, our results also have potential implications for ecosystem functioning given the

411   link between community functional structure and ecosystem processes, and more work is needed

412   to quantify the impact of functional redundancy on ecological functions. Finally, our work provides

413   guidance for marine resource management, demonstrating the need to maintain resilient functional

414   structures and high functional redundancy to conserve biodiversity under climate change.

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Acknowledgements

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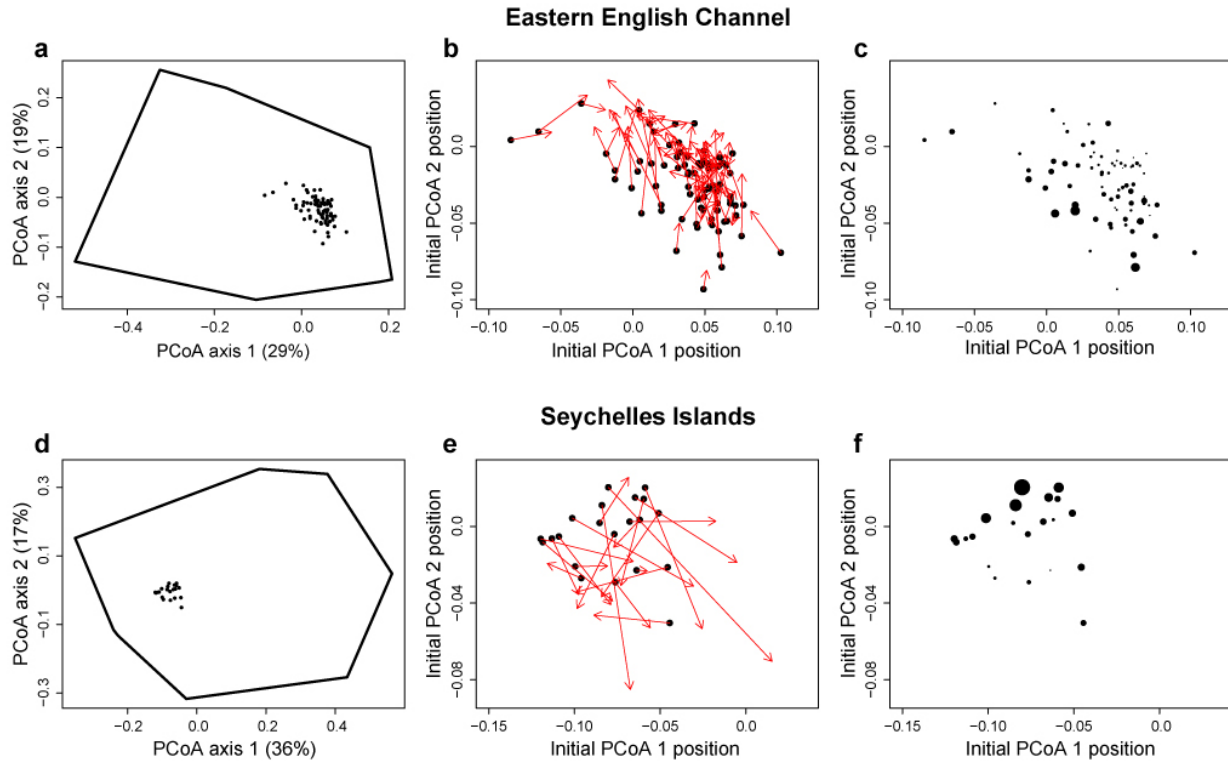630   109.

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637   **SUPPORTING INFORMATION**

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Supplementary Figure 1. Functional space with the movement of each site before and after the disturbance in both ecosystems. a) Convex hull of functional space in the Eastern English Channel with the initial position of all sites for the years before the disturbance. b) Arrows showing the movement of each site in functional space before and after the disturbance. c) Initial position of each site before the disturbance, with the size of each site scaled by the distance moved in functional space. a) Convex hull of functional space in the Seychelles Islands with the initial position of all sites for the years before the disturbance. b) Arrows showing the movement of each site in functional space before and after the disturbance. c) Initial position of each site before the disturbance, with the size of each site scaled by the distance moved in functional space.

Eastern English Channel

Seychelles Islands
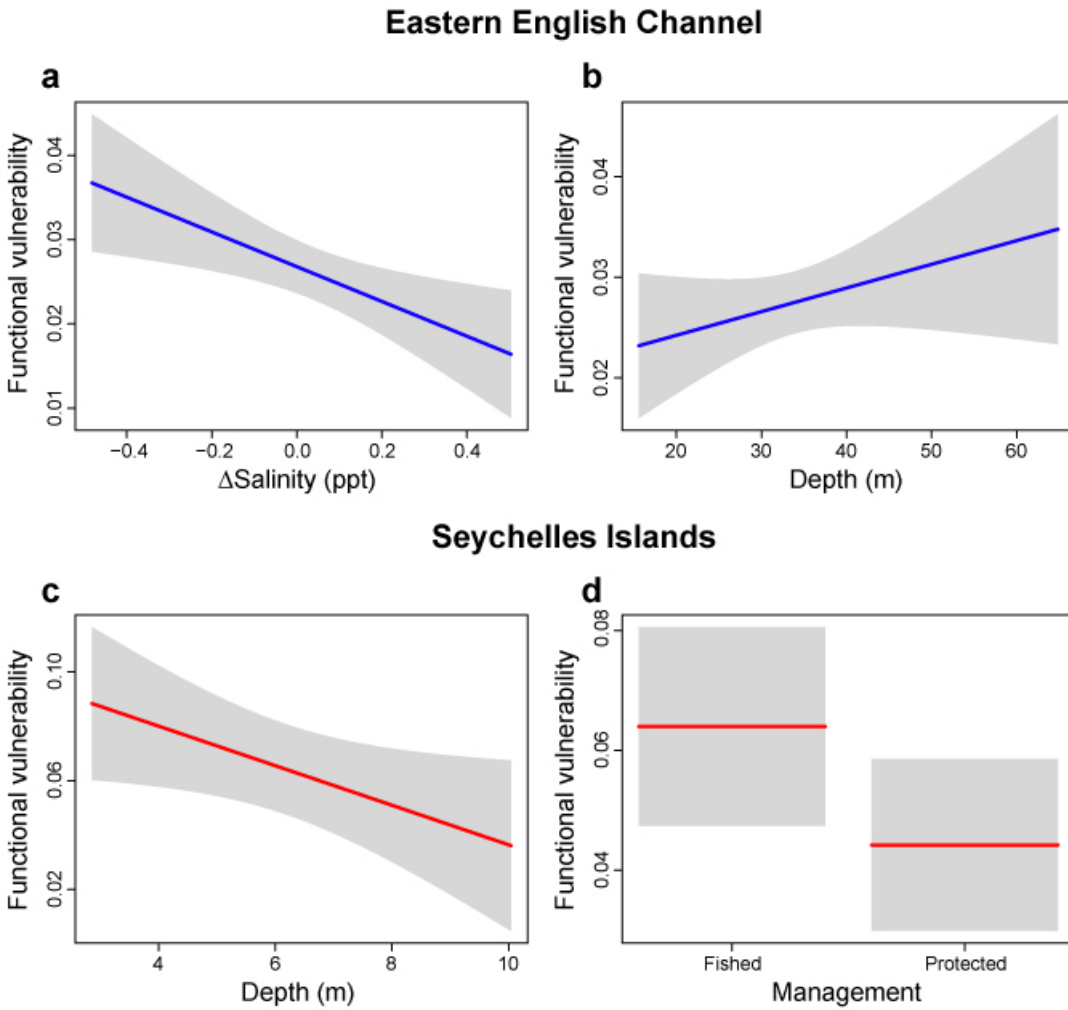
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651 **Supplementary Figure 2.** Relationship between the most influential environmental factors and
652 functional vulnerability in the Eastern English Channel (a,b) and Seychelles Islands (c,d).