

1 **Which traits are most responsive to environmental change:**
2 **interspecific differences blur trait dynamics in classic statistical**
3 **analyses**

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17 full-length papers or important experimental results that are not sufficiently elaborated or
18 developed as to justify an original paper. They may also present opinions or novel interpretation
19 of existing ideas.

20 **Abstract**

21 Trait-based ecology strives to better understand how species, through their bio-ecological traits,
22 respond to environmental changes and influence ecosystem functioning. Identifying which traits
23 are most responsive to environmental changes can provide insight for understanding community
24 structuring and developing sustainable management practices. However, misinterpretations are
25 possible because standard statistical methods (e.g., principal component analysis, linear
26 regression) for identifying and ranking the responses of different traits to environmental changes
27 ignore interspecific differences. Here, using both artificial data and real-world examples from
28 marine fish communities, we show how considering species-specific responses can lead to
29 drastically different results than standard community-level methods. By demonstrating the
30 potential impacts of interspecific differences on trait dynamics, we illuminate a major, yet rarely
31 discussed issue, highlighting how analytical misinterpretations can confound our basic
32 understanding of trait responses, which could have important consequences for biodiversity
33 conservation.

34

35 **Introduction**

36 Using species' traits, defined as any bio-ecological feature influencing individual performance in
37 a given environment (Violle et al. 2007), is widely advocated for understanding how biological
38 communities respond to environmental change. This requires identifying which traits exhibit the
39 greatest environmental responses and best characterize community dynamics (Lavorel and
40 Garnier 2002; McGill et al. 2006; Suding et al. 2008; Dehling et al. 2016; Gross et al. 2017).
41 Ranking the respective contribution of different traits to community responses can help identify

42 the ecological mechanisms structuring communities (Weiher and Keddy 1995; Pollock et al.
43 2012; Fort et al. 2014; Sakschewski et al. 2016). For example, in a marine fish community, if all
44 species increasing in abundance are related by high temperature preferences, we could likely
45 conclude that changes in community structure are primarily driven by ocean warming, and that
46 future increases in warm-adapted species are likely (Cheung et al. 2013). While this response-
47 trait approach is recognized for providing clearer information for planning conservation and
48 management efforts that are applicable across ecosystems and taxa (Díaz and Cabido 2001;
49 Winemiller et al. 2015; Pecuchet et al. 2017), proper interpretations of trait responses are critical.

50 Currently, descriptive statistics like ordination analyses are used to rank the respective
51 contributions of different traits to temporal and spatial community responses, i.e. which traits are
52 most responsive to environmental changes in time and space (Peres-Neto et al. 2003; Pla et al.
53 2011; Legendre and Legendre 2012). In temporal dynamics, principal component analysis (PCA)
54 is used to examine changes in a given community over time by examining the movement of the
55 community along the main principal component axes, while the most responsive traits are
56 inferred by ranking PCA loadings (Peres-Neto et al. 2003; Pla et al. 2011; Legendre and
57 Legendre 2012). Additionally, trait responsiveness can be inferred as the slope of the regression
58 between trait abundance and time or an environmental gradient (Noordijk et al. 2010; Jamil et al.
59 2014). From a purely descriptive standpoint, these methods provide accurate assessments of the
60 traits that explain the highest amount of variation in a dataset, and thus accurately identify the
61 traits with the greatest contributions to community variation in a statistical context. However,
62 using only such descriptive statistics can lead to misinterpretations of how traits respond to
63 environmental changes.

64 While ordination or regression-based methods might accurately indicate which trait
65 increased or decreased the most over time or space, this finding does not necessarily mean that

66 this trait was the most responsive to environmental changes. For example, if a certain trait
67 emerged as the most responsive because it had the greatest regression slope, this result could be
68 due to a single dominant species while all other species with this trait were unaffected, thus
69 questioning the unequivocal responsiveness of this group. For instance, ‘piscivore’ could be
70 identified as the trait most impacted by an environmental disturbance, yet if only one dominant
71 piscivore species decreased in abundance, while all remaining piscivores were unaffected we
72 have little confidence that piscivores are actually affected by this disturbance. Even though, under
73 the mass-ratio hypothesis, changes in the traits of the most abundant species should have the
74 highest impact on ecosystem processes owing to their dominance, it does not imply that they are
75 the most representative of how traits in general respond to changing environments (Grime 1998;
76 Díaz et al. 2007; Mokany et al. 2008). Rather, other traits could be far more responsive to
77 environmental changes, but simply less dominant in the community. Another problematic case
78 arises when a particular trait is shared by only a few species. If these species increase or decrease
79 synchronously in abundance just by chance, standard methods might indicate that the trait is
80 highly responsive while actually being a random signal (Peres-Neto et al. 2017). Instead, when a
81 trait is shared by many similarly affected species, we have greater confidence that this trait
82 contributes strongly to community responses, and is highly responsive to environmental change.

83 In this note we aim to point out that using standard statistical methods to identify which
84 traits are most responsive to environmental changes can lead to misinterpretations with important
85 consequences for anticipating changes in biodiversity. Such methods do not account for the
86 potential impacts of individual species, particularly dominant species and species with
87 inconsistent responses. Here, we illustrate the issues outlined above with a simulated case study
88 and two real-world examples using a basic index to rank the contribution of different trait groups
89 to community responses to environmental change.

90

91 **Materials and Methods**

92 **Trait group contributions to community responses**

93 Here ‘trait’ refers to any morphological, physiological or phenological feature related to
94 organismal fitness (Violle et al. 2007). In this study, for simplicity, we considered trait groups,
95 which are defined as groups of species with shared trait attributes (e.g., pelagic, demersal,
96 piscivore, planktivore, schooling, diurnal, oviparous, etc.). Thus, GROUPS were not chosen in
97 order to combine species with similar responses, but rather were defined according to shared bio-
98 ecological characteristics. This trait-based approach is commonly used to identify whether certain
99 shared characteristics explain how species respond to environmental perturbations (Engelhard et
100 al. 2011; McLean M et al. 2018). While considering GROUPS is most relevant for categorical
101 traits, it can be easily extended by grouping continuous traits, which is common in trait-based
102 studies (Mouillot et al. 2014; D’agata et al. 2016). However, it should be noted that the issues
103 outlined above apply equally to community-weighted mean approaches, particularly because
104 dominant species can drive changes in average trait values, masking the responses of other
105 species with similar trait values.

106 Here, we developed a simple index to demonstrate the potential misinterpretations of using
107 standard statistical methods that do not account for interspecific variation in environmental
108 responses. However, it should be noted that this index is used purely for demonstrative purposes
109 and is not proposed a solution for integrating interspecific differences into trait dynamics. This
110 simple index, hereafter called the trait response (TR) index, ranks trait group contributions to

111 temporal community dynamics. This index thus considers changes in community structure over
112 time and identifies the most responsive trait groups. This index has three complementary criteria:

- 113 i. The slope of the change in trait groups over time (i.e., Δ abundance or biomass time^{-1}).
- 114 ii. Kendall's coefficient of concordance, a measure of consistency among changes in
115 trait group member's abundances (i.e., whether species within a given trait group display
116 similar dynamics), ranging from 0 to 1 (Legendre 2005). When the coefficient is 1, all
117 species display the same type of change; when the coefficient is 0, there is no
118 consistency among species, and the dynamics of the corresponding trait group are
119 essentially random. Kendall's coefficient is calculated by rank-ordering the
120 abundances of each species across years, and consistency among species' abundance
121 rankings within each group is computed via the mean and sum of squared deviations of
122 the rankings (see Legendre 2005).
- 123 iii. The number of species whose temporal trends (increase vs. decrease in abundance) are the
124 same as the overall GROUP to which they belong, i.e., if the overall GROUP decreased in
125 abundance, the number of species in this group that decreased in abundance. This
126 component first adds a probabilistic aspect, reinforcing that higher numbers of
127 species with consistent responses reduce the likelihood that trait group dynamics are
128 due to chance alone. Secondly, it complements Kendall's concordance, which can be
129 equal for groups with different numbers of species. For example, GROUPS
130 consisting of singletons or doubletons could show very high slopes and have 100%
131 response consistency, however, having only 1 to 2 species limits our confidence that this
132 group is truly responsive, whereas a higher number of species showing consistent
133 responses increases our confidence.

134 The TR index is then calculated as the absolute value of the product of these three criteria
135 according to the following formula:

$$136 \quad TR_i = |m_i \times W_i \times n_i|$$

137 where i is a given trait group, m is the regression slope of the change in the trait group (i.e.,
138 abundance or biomass; Fig. 1e) through time, W is Kendall's coefficient for the trait group, and n
139 is the number of species in the group that have the same temporal trend as the overall group itself
140 (i.e., increase or decrease). This index produces a unit-less value (that ranges between 0 and ∞)
141 that is used to rank the overall contributions of each trait group to changes in community
142 structure over time, i.e., to identify the most responsive trait groups. The absolute value is used in
143 order to rank trait group responses regardless of whether groups increase or decrease. Higher
144 values of the index correspond to groups with strong responsiveness, while lower values
145 correspond to groups with weak responsiveness due to either low abundance changes, low
146 consistency among species, or low species count.

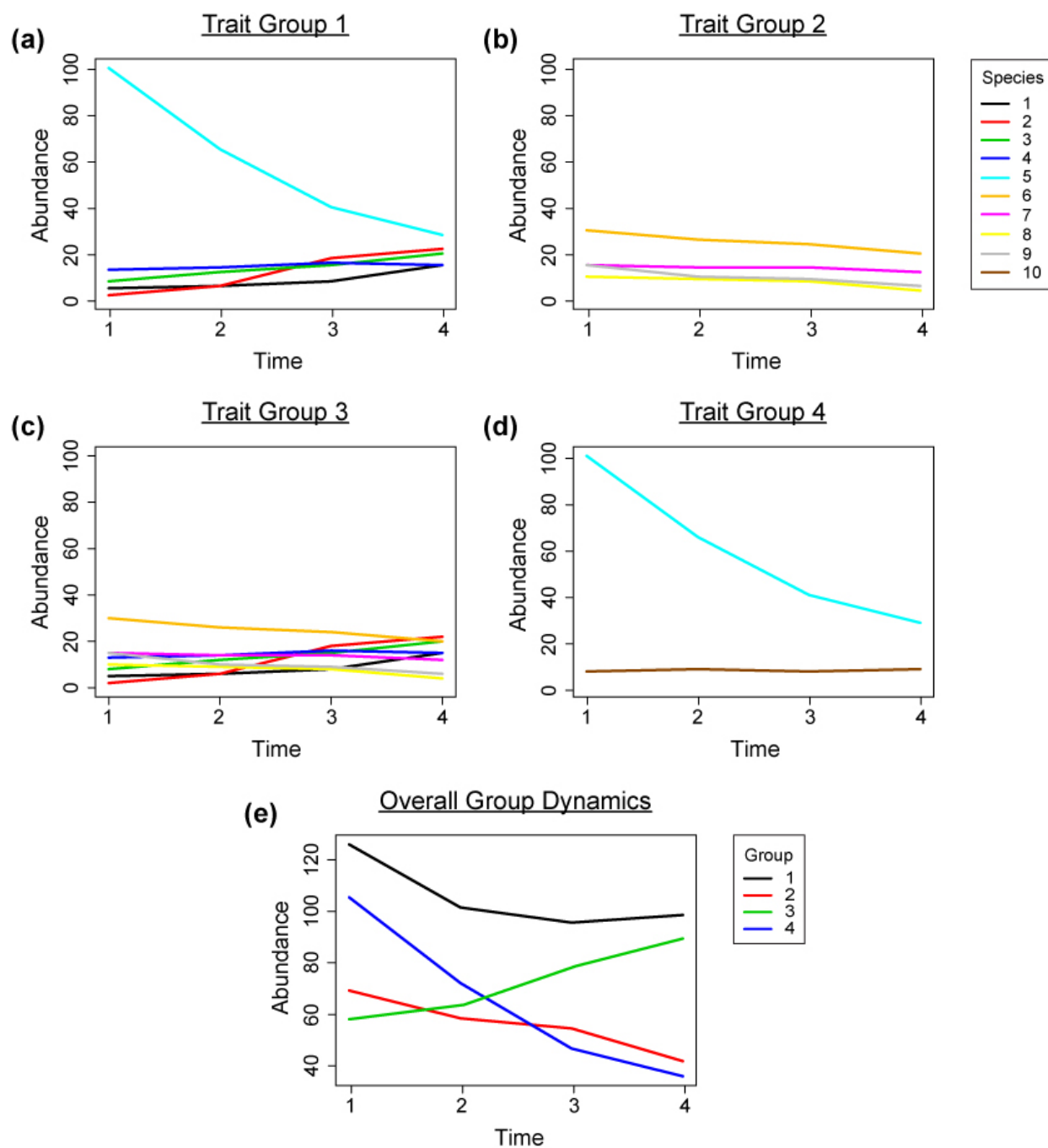
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148 **Simulated case study**

149 To qualitatively demonstrate the problems outlined in the introduction, we first created artificial
150 datasets of species' abundances and traits, where we considered changes in the abundance of ten
151 species comprising four trait groups over four years (note that some species belonged to more
152 than one group) (Fig. 1a-d). For this theoretical example, species abundances were specifically
153 (i.e., non-randomly) chosen to highlight the case of a right-skewed community distribution due to
154 many rare and one dominant species, and the potential impact this can have on analytical
155 interpretations. Thus we allocated large decreasing abundances to a single species, and assigned

156 lower abundances to all other species. We furthermore adjusted species' abundances so that three
157 of the trait groups had low response consistency among species (groups 1, 3, and 4), while one
158 trait group had high consistency (group 2). Temporal dynamics of the trait groups (Fig. 1e) were
159 first calculated using the two standard methods – the slope of the abundance of each trait group
160 over time and the PCA loadings of each group. The TR index was then calculated and trait group
161 contribution rankings were compared across the three methods.

162



163
 164 **Fig. 1** Temporal dynamics of ten artificial species belonging to four different trait groups **a-d**,
 165 and the resulting dynamics of the trait groups themselves **e**. Artificial data were created to
 166 highlight the case where a single dominant species drives trait group dynamics (species #5), and
 167 where response consistency is low among trait group members **a, c, d**.

168

169 **Real-world example 1: reef fish responses to coral bleaching**

170 We next examined coral-reef fish dynamics following a mass coral bleaching event, specifically
171 examining which trait groups were most impacted by coral mortality. The Seychelles Islands
172 experienced wide-spread coral mortality following severe bleaching during the 1998 El Nino
173 event, which led to substantial changes in benthic structure and reef fish community composition
174 (Graham et al. 2015). Fish abundance data were collected at 21 sites around the Seychelles
175 Islands using underwater visual census (UVC) in both 1994 (pre-bleaching) and 2005 (post-
176 bleaching). Abundance data were collected for 129 species, which were assigned to six trait
177 groups according to species' main diets: predators, invertivores, planktivores, grazing herbivores
178 (grazers), scraping herbivores (scrapers), and corallivores (Graham et al. 2015). Because
179 dominant species can bias GROUP dynamics, all species abundances were $\log_{10}(x+1)$
180 transformed before analyses. Standard data transformations such as log and Hellinger can
181 strongly alleviate the influence of dominant species; however, data transformations cannot
182 entirely resolve the issues outlined in the introduction, as species' abundances often vary by
183 several orders of magnitude. The TR index was then calculated and trait group rankings were
184 compared with the rankings from the absolute value of slope and PCA loadings.

185

186 **Real-world example 2: long-term changes in North Sea fish communities**

187 We next applied the TR index to long-term fish community data in the southern North Sea, again
188 examining which diet groups were most responsive to environmental changes through time. The
189 southern North Sea has experienced significant community change in the last thirty years due to
190 sea surface warming, with marked increases in warm-adapted species (Dulvy et al. 2008;
191 Engelhard et al. 2011; Cheung et al. 2013). Fish abundance data have been collected annually
192 since 1983 across the entire North Sea during the fisheries monitoring campaign the International
193 Bottom Trawl Survey (Verin 1992). Here we included data for the southern North Sea (area

194 approximately south of the 50-m depth contour; Pecuchet et al. 2017; McLean et al. 2018)
195 ranging from 1983 to 2015 for 110 species. Species were assigned to five trait groups according
196 to their main diets: piscivores, benthopiscivores, carcinophages (crab-eating), benthivores, and
197 planktivores. All species abundances were $\log_{10}(x+1)$ transformed before analyses. We then
198 calculated and compared the TR trait group rankings against rankings of the absolute value of
199 slope and PCA loadings.

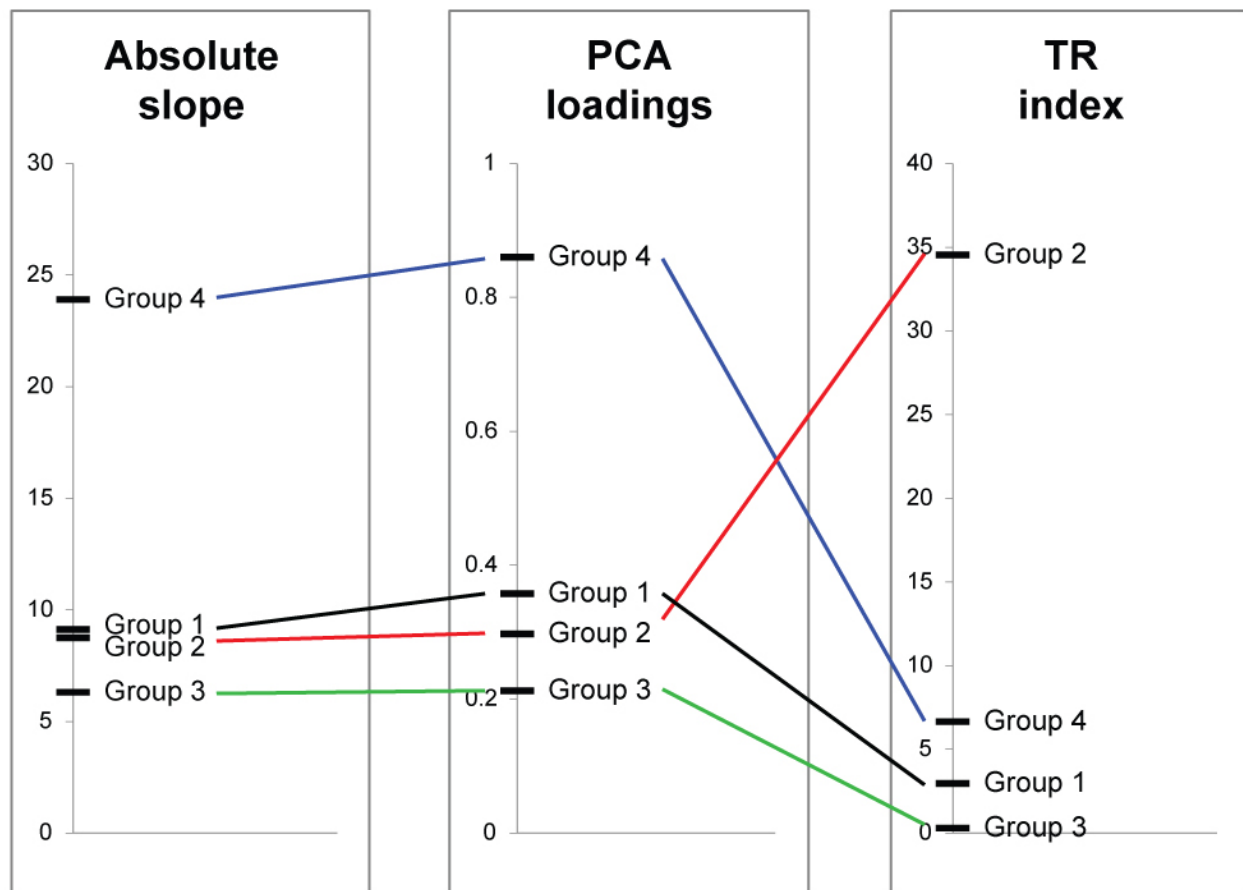
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201 **Results**

202 **Simulated case study**

203 Trait group #4 was ranked as the group with the greatest contribution to temporal community
204 dynamics, i.e. the most responsive trait, by both the slope of trait group abundance and by PCA
205 loadings (Fig. 2). However, further examination revealed that this pattern was driven by the
206 abundance of the single dominant species (#5) (Fig. 1d). Using the TR index, however, group #4
207 dropped from most responsive to second, while group #2 rose from third to first (Fig. 2). While
208 group #2 did not have the greatest change in overall abundance, this group included nearly half
209 the species, all of which decreased in abundance (Fig. 1b). These results highlight the potential
210 discrepancy between standard community-level methods and methods that consider interspecific
211 differences. Here, by considering the response of each species within a trait group rather than the
212 total abundance of the group itself, we found that group #2 was much more representative of
213 community responses as all species within this group had the same dynamics (i.e., decreased in
214 abundance).

215



216

217 **Fig. 2** Comparison of slope, PCA loadings, and the TR index for assessing the contributions of
 218 individual trait groups to the temporal responses of an artificial community of ten species
 219 comprising four trait groups.

220

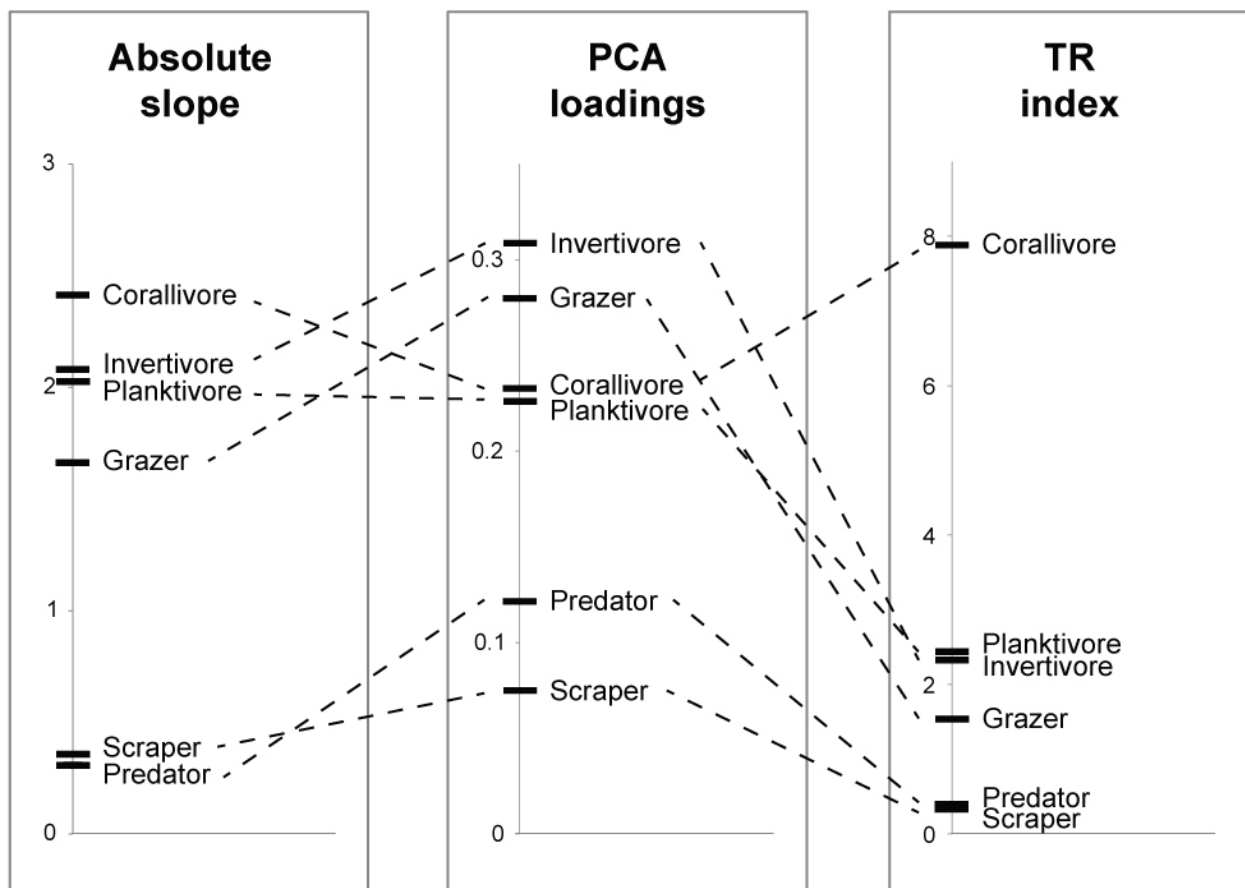
221 Reef fish responses to coral bleaching

222 All six trait groups decreased in abundance between 1994 and 2005 following the wide-spread
 223 coral bleaching event. The absolute value of slope ranked corallivores as the trait group with the
 224 greatest contribution to community responses (i.e., the most responsive trait), followed closely by
 225 invertivores, planktivores, and grazers, while scrapers and predators had weak responses. PCA
 226 loadings, on the other hand, ranked invertivores and grazers as the most responsive groups, while
 227 corallivores and planktivores had lesser and nearly equal rankings, and predators and scrapers
 228 again had weak responses (Fig. 3). Using the TR index, corallivores were ranked as the most

229 responsive group, substantially above all other groups in relative importance, while invertivores,
 230 grazers, and planktivores all dropped markedly and had similar responses (Fig. 3). While both
 231 slope and the TR index ranked corallivores as the most responsive trait group, the relative
 232 importance of corallivores in comparison to invertivores and planktivores was much higher for
 233 the TR index. In contrast, PCA loadings originally ranked invertivores and grazers as the most
 234 responsive groups based on their prevalence and dominant abundances; however, following
 235 massive loss of live corals, corallivores were clearly most impacted, as all species were similarly
 236 impacted despite their lesser abundances.

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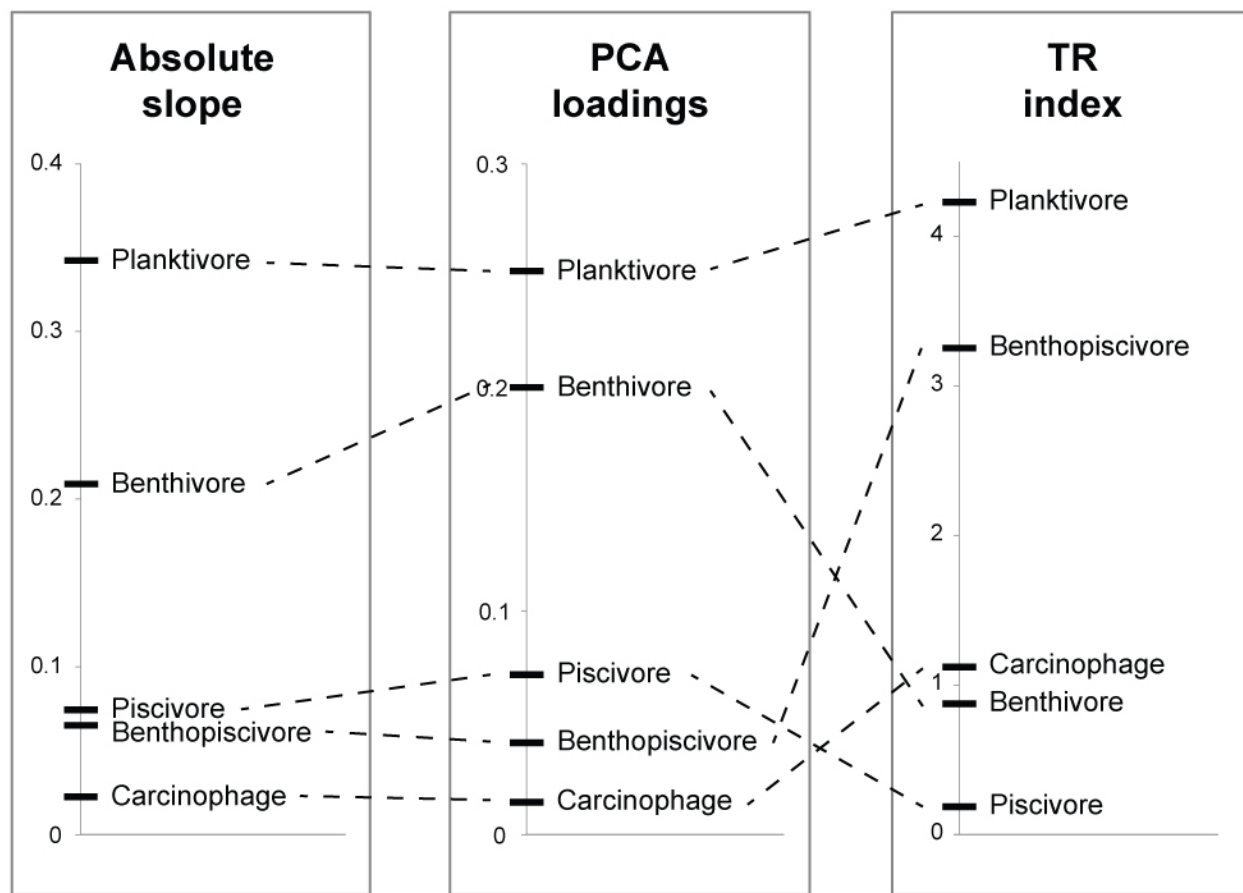
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240 **Fig. 3** Comparison of slope, PCA loadings, and the TR index for assessing the contributions of
241 reef-fish trait groups to community responses following mass coral mortality due to coral-
242 bleaching.
243

244 **Long-term changes in North Sea fish communities**

245 All five trait groups increased in abundance over time. Using slope and PCA loadings,
246 planktivores were ranked as the trait group contributing most to community responses in the
247 southern North Sea, followed closely by benthivores, with piscivores, benthopiscivores, and
248 lastly carcinophages having lower contributions (Fig. 4). Using the TR index, planktivores
249 remained the most responsive group; however benthivores dropped substantially, from second to
250 fourth, while benthopiscivores rose from fourth to second (Fig. 4). Carcinophages also rose from
251 fifth to third, while piscivores dropped to last. Thus, when considering species-specific responses,
252 benthopiscivores were much more responsive to long-term environmental changes in the southern
253 North Sea than benthivores, and carcinophages were more responsive than piscivores.

254



255

256 **Fig. 4** Comparison of slope, PCA loadings, and the TR index for assessing the contributions of
 257 trait groups to long-term community responses in the northern North Sea.

258

259 Discussion

260 Our results draw attention to the danger of statistically examining trait dynamics without
 261 considering interspecific differences, especially when communities are composed of few
 262 dominant and many rare species. Here, we show that using different methods to examine the
 263 same trends can lead to markedly different rankings of the trait groups that are most responsive to
 264 environmental changes. Incorporating basic concepts like species dominance and response
 265 consistency among trait group members lead to different results than standard community-level
 266 methods and highlighted the importance of considering species-specific responses when
 267 analyzing trait dynamics.

268 While rarely discussed in current literature, ignoring the potential impacts of individual
269 species responses, notably dominant species and species with inconsistent dynamics, can greatly
270 bias statistical results and remains a prevalent issue in trait-based studies. Numerous studies
271 examining temporal changes in communities' trait structures use methods such as PCA,
272 redundancy analysis (RDA), or RLQ analysis, which are all heavily influenced by dominant
273 species. Additionally, while we examined trait groups according to categorical traits, applying
274 such methods to community-weighted mean trait values rather than trait groups does not relieve
275 the issue, as major changes in trait dominance can be entirely driven by single species (Bello et
276 al. 2007, 2012; Nickerson et al. 2018). While recent approaches have been developed to identify
277 the contribution of different species to changes in a single community-weighted mean trait (e.g.,
278 temperature preference) (Princé and Zuckerberg 2015; Gaüzère et al. 2019), this issue remains
279 unresolved for multi-trait approaches. Here, for simplicity, we examined changes in multiple trait
280 groups within the single trait 'diet,' however, integrating multiple traits is necessary to fully
281 characterize community responses to environmental change (Lefcheck et al. 2015). Studies
282 examining fish community dynamics generally integrate several traits such as habitat use, diet,
283 body size, and reproductive mode (Frainer et al. 2017; Pecuchet et al. 2018; McLean et al. 2019).
284 Identifying the traits that are most responsive to environmental changes (rather than identifying
285 the species that contribute most to changes in a single trait) in such multi-trait studies is
286 substantially more difficult, as multi-trait dynamics are clearly blurred by interspecific
287 differences.

288 Furthermore, choosing and assigning traits to different species can have a major impact on
289 results depending on the dominance and dynamics of the species. For example, when a dominant
290 species is both a planktivore and a piscivore depending on ontogeny and resource availability, if
291 the species is classified as a piscivore and has major changes in abundance, the overall

292 conclusion will be that piscivores are heavily impacted by disturbance, even though this result
293 was driven by a single opportunistic species. While seemingly intuitive, such issues remain
294 widespread in trait-based studies and their potential consequences are rarely considered.

295 A central goal of trait-based ecology is to understand how organisms respond to
296 environmental gradients, notably to anticipate future biodiversity changes (Keddy 1992; Weiher
297 and Keddy 1995; McGill et al. 2006; Winemiller et al. 2015). As the global environment
298 continues to change due to both human-induced and natural environmental pressures,
299 understanding how different trait groups will respond is critical to planning how we will adapt
300 conservation and management efforts to maintain ecosystem services (Vitousek et al. 1997;
301 Hulme et al. 1999; Edwards and Richardson 2004; Thuiller et al. 2006; Poloczanska et al. 2013).
302 As the power of trait-based ecology lies in understanding fundamental trait-environment
303 relationships, we must consider ecological implications, like species-specific responses, to a
304 greater extent in statistical methods. The greatest potential danger lies in misidentifying traits that
305 are most responsive to environmental changes, especially for resource management. For instance,
306 in the artificial example, standard methods identified trait group #4 as the most responsive, which
307 could lead to the conclusion that group #4 is the most characteristic of the community response.
308 Thus, resource managers might mistakenly believe that environmental changes most prominently
309 impact communities through decreases in species in group #4, when in fact decreases in species
310 in group #2 are much more representative. By misidentifying trait-environment relationships
311 driven by dominant species, resource managers could be ill-prepared for sudden changes in
312 community structure driven by rare species.

313 In our reef fish example, an ecosystem at the forefront of climatic disturbance (Graham et
314 al. 2015; Hughes et al. 2018), standard statistical methods (i.e., PCA) could support the
315 conclusion that invertivores are the most responsive trophic group to coral bleaching, leading to

316 potential misallocation of resources, when in reality corallivores are much more responsive and
317 present a more critical management target. In the southern North Sea, an ecosystem highly
318 impacted by climate warming (Dulvy et al. 2008; Engelhard et al. 2011; McLean et al. 2018),
319 standard methods would conclude that benthopiscivorous species have been relatively
320 unimportant to community dynamics through time and are thus unresponsive to sea surface
321 warming, when in reality this group has shown consistent, positive responses. These examples
322 highlight how our basic understanding of community responses to climate change can be
323 compromised if we fail to consider the interspecific differences behind trait dynamics.

324 As our primary objective in this concept paper was not to develop a new method for
325 examining trait dynamics, but to highlight potential issues arising from standard methods, we
326 acknowledge that the index used here is both basic and imperfect, and alternatives with other
327 ecological criteria and different mathematical structures are feasible. For example, while our
328 index was based on consistency among GROUP members using Kendall's coefficient of
329 concordance, this approach cannot account for competition among species within groups, or
330 functional replacement by unaffected species within the same group (i.e., via functional
331 redundancy). However, we reconcile that groups containing species that show inconsistent
332 environmental responses (i.e., some decrease while others increase) due to competitive release or
333 functional replacement are likely not the most environmentally-responsive groups given that
334 some species suffer while others benefit. Rather, other traits may better explain why species
335 increased or decreased in abundance, and GROUPS where nearly all species are similarly
336 affected are likely more responsive. Kendall's concordance may also not be well adapted for
337 hyper-diverse regions because too many species packed within few GROUPS could mask the
338 responses of highly impacted GROUP members. We therefore encourage others to propose
339 additional ecological criteria relevant to examining trait dynamics and to develop alternative

340 methods that build on the concepts presented here. Furthermore, with the goal of accurately
341 identifying trait group responses to environmental change, additional approaches focusing on the
342 underlying mechanisms of trait responses will greatly increase our understanding of trait-
343 environment relationships. Laboratory studies examining how different trait groups, and their
344 constituent species, respond to environmental variation like sea-surface warming can more
345 concretely determine which traits are truly most sensitive to environmental changes, and identify
346 the physiological characteristics linking these traits (Ospina and Mora 2004; Sandblom et al.
347 2014; Verberk et al. 2016; Messmer et al. 2017). Such understanding will be critical for
348 anticipating the ecological impacts of global environmental change.

349 The examples in this concept paper bring to light a specific case in prioritizing trait group
350 contributions, but also draw attention to the larger issue of framing data analyses and
351 interpretations in ecological contexts. While many powerful tools are readily available to
352 contemporary ecologists, the corresponding results are only as good as the interpretations they
353 permit. As trait-based ecology continues to expand, it is important that we consider the ecological
354 contexts of methods and results in order to generate trait-environmental relationships that
355 accurately reflect community dynamics, a critical step for better understanding ecosystem
356 functioning.

357

358 **Compliance with Ethical Standards**

359 The authors declare no conflict of interest. All applicable international, national and/or
360 institutional guidelines for sampling, care and experimental use of organisms for the study were
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362

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368 **References**

- 369 Cheung WW, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch.
370 *Nature* 497:365–368.
- 371 D’agata S, Vigliola L, Graham NAJ, Wantiez L, Parravicini V, Villéger S, Mou-Tham G, Frolla
372 P, Friedlander AM, Kulbicki M, Mouillot D (2016) Unexpected high vulnerability of
373 functions in wilderness areas: evidence from coral reef fishes. *Proc R Soc B Biol Sci*
374 283:20160128. doi: 10.1098/rspb.2016.0128
- 375 de Bello F, Lepš J, Lavorel S, Moretti M (2007) Importance of species abundance for assessment
376 of trait composition: an example based on pollinator communities. *Community Ecol*
377 8:163–170.
- 378 de Bello F, Lavorel S, Lavergne S, Albert CH, Boulangéat I, Mazel F, Thuiller W (2012)
379 Hierarchical effects of environmental filters on the functional structure of plant
380 communities: a case study in the French Alps. *Ecography* 36:393–402. doi:
381 10.1111/j.1600-0587.2012.07438.x
- 382 Dehling DM, Jordano P, Schaefer HM, Böhning-Gaese K, Schleuning M (2016) Morphology
383 predicts species’ functional roles and their degree of specialization in plant–frugivore
384 interactions. *Proc R Soc B Biol Sci*. doi: 10.1098/rspb.2015.2444
- 385 Díaz S, Lavorel S, de Bello F, Quétier F, Grigulis K, Robson TM (2007) Incorporating plant
386 functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci*
387 104:20684–20689.
- 388 Díaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem
389 processes. *Trends Ecol Evol* 16:646–655.

- 390 Dulvy NK, Rogers SI, Jennings S, Stelzenmiller V, Dye SR, Skjoldal HR (2008) Climate change
391 and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J*
392 *Appl Ecol* 45:1029–1039. doi: 10.1111/j.1365-2664.2008.01488.x
- 393 Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and
394 trophic mismatch. *Nature* 430:881.
- 395 Engelhard GH, Ellis JR, Payne MR, ter Hofstede R, Pinnegar JK (2011) Ecotypes as a concept
396 for exploring responses to climate change in fish assemblages. *ICES J Mar Sci* 68:580–
397 591. doi: 10.1093/icesjms/fsq183
- 398 Fort F, Cruz P, Jouany C (2014) Hierarchy of root functional trait values and plasticity drive
399 early-stage competition for water and phosphorus among grasses. *Funct Ecol* 28:1030–
400 1040.
- 401 Frainer A, Primicerio R, Kortsch S, Aune M, Dolgov AV, Fossheim M, Aschan MM (2017)
402 Climate-driven changes in functional biogeography of Arctic marine fish communities.
403 *Proc Natl Acad Sci* 114:12202–12207.
- 404 Gaüzère P, Doucier G, Devictor V, Kéfi S (2019) A framework for estimating species-specific
405 contributions to community indicators. *Ecol Indic* 99:74–82.
- 406 Graham NA, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven
407 regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97.
- 408 Grime J (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J*
409 *Ecol* 86:902–910.
- 410 Gross N, Le Bagousse-Pinguet Y, Liancourt P, Berdugo M, Gotelli NJ, Maestre FT (2017)
411 Functional trait diversity maximizes ecosystem multifunctionality. *Nat Ecol Evol* 1:0132.
- 412 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK,
413 Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H,
414 Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM,
415 Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of
416 mass bleaching of corals in the Anthropocene. *Science* 359:80. doi:
417 10.1126/science.aan8048
- 418 Hulme M, Barrow EM, Arnell NW, Harrison PA, Johns TC, Downing TE (1999) Relative
419 impacts of human-induced climate change and natural climate variability. *Nature*
420 397:688–691.
- 421 Jamil T, Kruk C, ter Braak CJF (2014) A Unimodal Species Response Model Relating Traits to
422 Environment with Application to Phytoplankton Communities. *PLOS ONE* 9:e97583.
423 doi: 10.1371/journal.pone.0097583
- 424 Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. *J*
425 *Veg Sci* 3:157–164. doi: 10.2307/3235676

- 426 Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem
427 functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16:545–556.
- 428 Lefcheck JS, Bastazini VA, Griffin JN (2015) Choosing and using multiple traits in functional
429 diversity research. *Environ Conserv* 42:104–107.
- 430 Legendre P (2005) Species associations: the Kendall coefficient of concordance revisited. *J Agric
431 Biol Environ Stat* 10:226–245.
- 432 Legendre P, Legendre LF (2012) *Numerical ecology*. Elsevier
- 433 McGill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from
434 functional traits. *Trends Ecol Evol* 21:178–185. doi: 10.1016/j.tree.2006.02.002
- 435 McLean M, Mouillot D, Lindegren M, Engelhard G, Villéger S, Marchal P, Brind'Amour A,
436 Auber A (2018) A Climate-Driven Functional Inversion of Connected Marine
437 Ecosystems. *Curr Biol* 28:3654–3660.e3. doi: 10.1016/j.cub.2018.09.050
- 438 McLean M, Mouillot D, Auber A (2018) Ecological and life history traits explain a climate-
439 induced shift in a temperate marine fish community. *Mar Ecol Prog Ser* 606:175–186.
- 440 McLean MJ, Mouillot D, Goascoz N, Schlaich I, Auber A (2019) Functional reorganization of
441 marine fish nurseries under climate warming. *Glob Change Biol* 25:660–674. doi:
442 10.1111/gcb.14501
- 443 Messmer V, Pratchett MS, Hoey AS, Tobin AJ, Coker DJ, Cooke SJ, Clark TD (2017) Global
444 warming may disproportionately affect larger adults in a predatory coral reef fish. *Glob
445 Change Biol* 23:2230–2240. doi: 10.1111/gcb.13552
- 446 Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in
447 influencing ecosystem processes in a temperate native grassland. *J Ecol* 96:884–893.
- 448 Mouillot D, Villéger S, Parravicini V, Kulbicki M, Arias-Gonzalez JE, Bender M, Chabanet P,
449 Floeter SR, Friedlander A, Vigliola L, Bellwood DR (2014) Functional over-redundancy
450 and high functional vulnerability in global fish faunas on tropical reefs. *Proc Natl Acad
451 Sci* 111:13757–13762. doi: 10.1073/pnas.1317625111
- 452 Nickerson KJ, Grothues TM, Able KW (2018) Sensitivity of a fish time-series analysis to guild
453 construction: a case study of the Mullica River-Great Bay ecosystem. *Mar Ecol Prog Ser
454* 598:113–129.
- 455 Noordijk J, Musters CJM, van Dijk J, de Snoo GR (2010) Invertebrates in field margins:
456 taxonomic group diversity and functional group abundance in relation to age. *Biodivers
457 Conserv* 19:3255–3268. doi: 10.1007/s10531-010-9890-1
- 458 Ospina AF, Mora C (2004) Effect of body size on reef fish tolerance to extreme low and high
459 temperatures. *Environ Biol Fishes* 70:339–343.

- 460 Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzón
461 A, Sólmundsson J, Payne MR (2017) From traits to life-history strategies: Deconstructing
462 fish community composition across European seas. *Glob Ecol Biogeogr* 26:812–822. doi:
463 10.1111/geb.12587
- 464 Pecuchet L, Reygondeau G, Cheung WWL, Licandro P, van Denderen PD, Payne MR, Lindegren
465 M (2018) Spatial distribution of life-history traits and their response to environmental
466 gradients across multiple marine taxa. *Ecosphere* 9:e02460. doi: 10.1002/ecs2.2460
- 467 Peres-Neto PR, Jackson DA, Somers KM (2003) Giving meaningful interpretation to ordination
468 axes: assessing loading significance in principal component analysis. *Ecology* 84:2347–
469 2363.
- 470 Peres-Neto PR, Dray S, ter Braak CJF (2017) Linking trait variation to the environment: critical
471 issues with community-weighted mean correlation resolved by the fourth-corner
472 approach. *Ecography* 40:806–816. doi: 10.1111/ecog.02302
- 473 Pla L, Casanoves F, Di Rienzo J (2011) Quantifying functional biodiversity. Springer Science &
474 Business Media
- 475 Pollock LJ, Morris WK, Vesk PA (2012) The role of functional traits in species distributions
476 revealed through a hierarchical model. *Ecography* 35:716–725.
- 477 Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K,
478 Bruno JF, Buckley LB, Burrows MT (2013) Global imprint of climate change on marine
479 life. *Nat Clim Change* 3:919–925.
- 480 Princé K, Zuckerberg B (2015) Climate change in our backyards: the reshuffling of North
481 America’s winter bird communities. *Glob Change Biol* 21:572–585. doi:
482 10.1111/gcb.12740
- 483 Sakschewski B, von Bloh W, Boit A, Poorter L, Peña-Claros M, Heinke J, Joshi J, Thonicke K
484 (2016) Resilience of Amazon forests emerges from plant trait diversity. *Nat Clim Change*
485 6:1032–1036. doi: 10.1038/nclimate3109
- 486 Sandblom E, Gräns A, Axelsson M, Seth H (2014) Temperature acclimation rate of aerobic scope
487 and feeding metabolism in fishes: implications in a thermally extreme future. *Proc R Soc*
488 *B Biol Sci*. doi: 10.1098/rspb.2014.1490
- 489 Suding KN, Lavorel S, Chapin FS, Cornelissen JHC, Díaz S, Garnier E, Goldberg D, Hooper
490 DU, Jackson ST, Navas M-L (2008) Scaling environmental change through the
491 community-level: a trait-based response-and-effect framework for plants. *Glob Change*
492 *Biol* 14:1125–1140. doi: 10.1111/j.1365-2486.2008.01557.x
- 493 Thuiller W, Lavorel S, Sykes MT, Araújo MB (2006) Using niche-based modelling to assess the
494 impact of climate change on tree functional diversity in Europe. *Divers Distrib* 12:49–60.

- 495 Verberk WCEP, Durance I, Vaughan IP, Ormerod SJ (2016) Field and laboratory studies reveal
496 interacting effects of stream oxygenation and warming on aquatic ectotherms. *Glob*
497 *Change Biol* 22:1769–1778. doi: 10.1111/gcb.13240
- 498 Verin Y (1992) IBTS: International Bottom Trawl Survey. doi: 10.18142/17
- 499 Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the
500 concept of trait be functional! *Oikos* 116:882–892. doi: 10.1111/j.0030-
501 1299.2007.15559.x
- 502 Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's
503 ecosystems. *Science* 277:494–499.
- 504 Weiher E, Keddy PA (1995) Assembly Rules, Null Models, and Trait Dispersion: New Questions
505 from Old Patterns. *Oikos* 74:159. doi: 10.2307/3545686
- 506 Winemiller KO, Fitzgerald DB, Bower LM, Pianka ER (2015) Functional traits, convergent
507 evolution, and periodic tables of niches. *Ecol Lett* 18:737–751. doi: 10.1111/ele.12462