1 **Which traits are most responsive to environmental change:**

2 **interspecific differences blur trait dynamics in classic statistical**

3 **analyses**

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16 **Article type:** Short note: brief papers that contain significant observations that do not warrant

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 owning 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

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:

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

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.

147

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.

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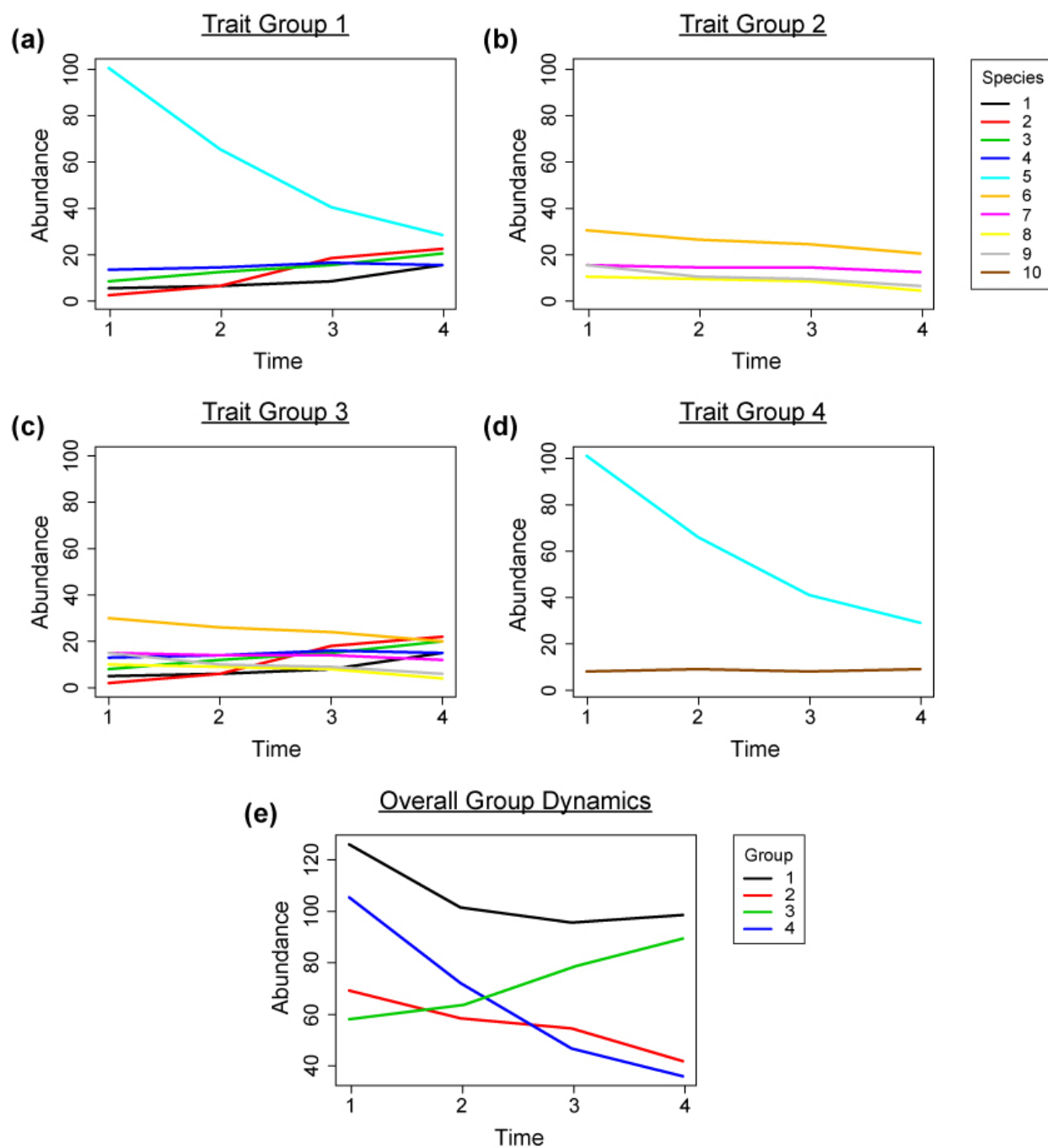
Fig. 1 Temporal dynamics of ten artificial species belonging to four different trait groups **a-d**, and the resulting dynamics of the trait groups themselves **e**. Artificial data were created to highlight the case where a single dominant species drives trait group dynamics (species #5), and where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

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 log10(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 log10(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.

200

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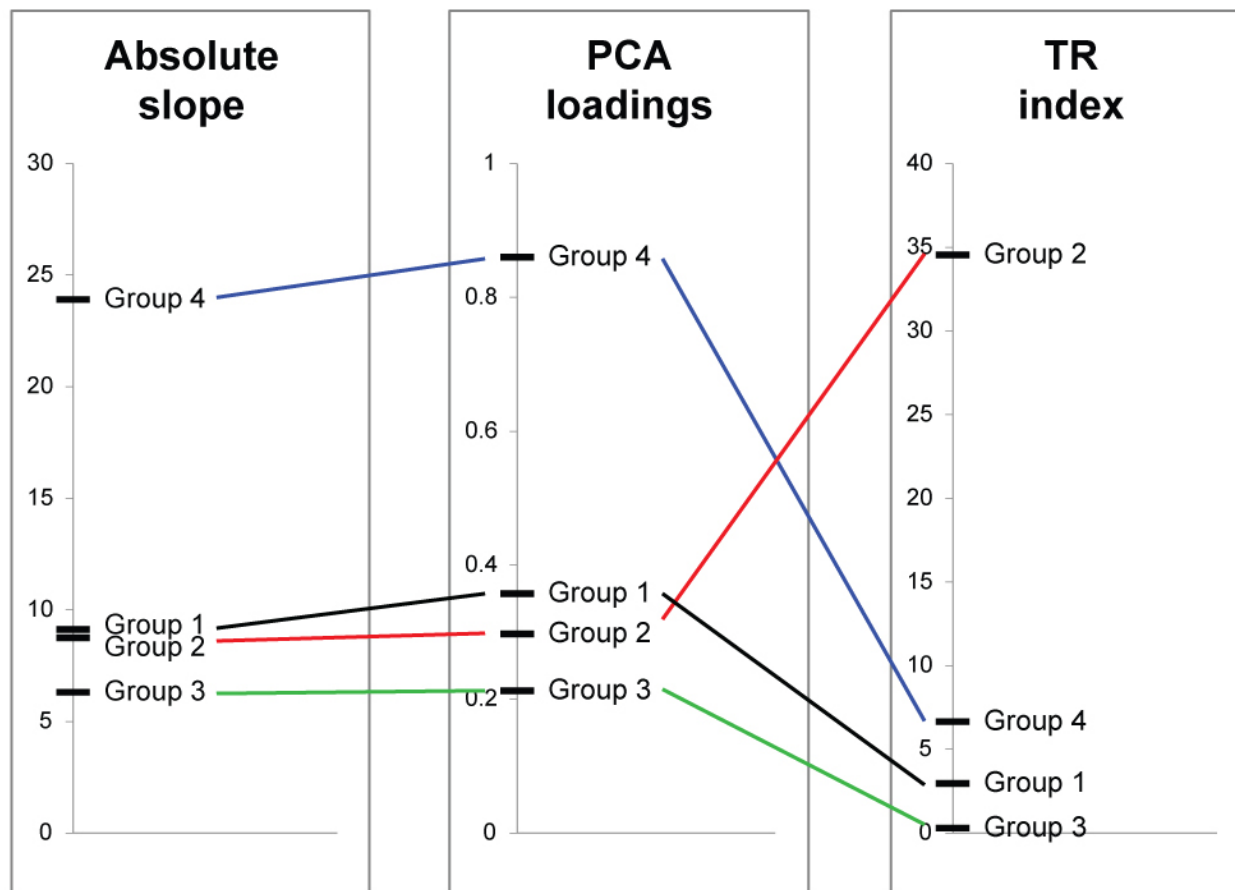
Fig. 2 Comparison of slope, PCA loadings, and the TR index for assessing the contributions of individual trait groups to the temporal responses of an artificial community of ten species comprising four trait groups.

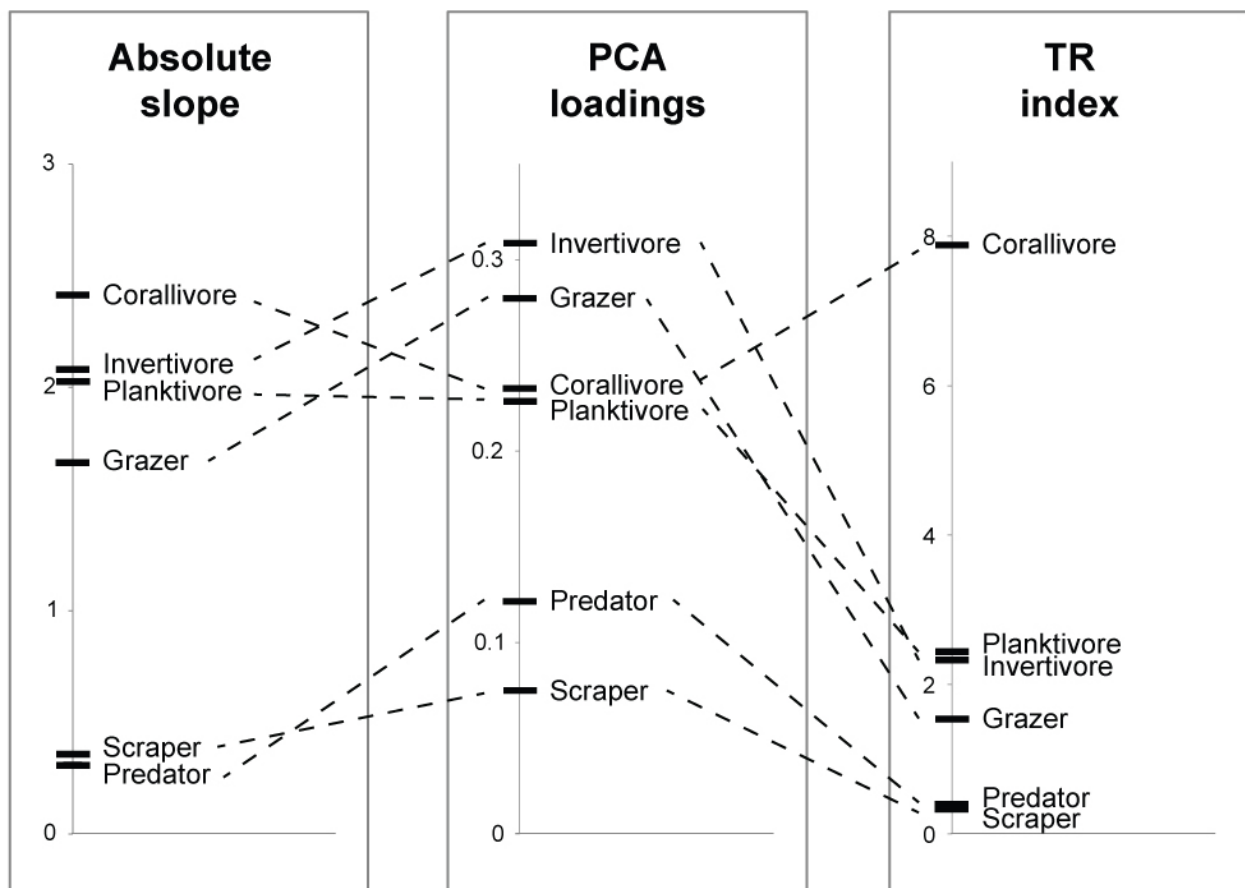**Reef fish responses to coral bleaching**

All six trait groups decreased in abundance between 1994 and 2005 following the wide-spread coral bleaching event. The absolute value of slope ranked corallivores as the trait group with the greatest contribution to community responses (i.e., the most responsive trait), followed closely by invertivores, planktivores, and grazers, while scrapers and predators had weak responses. PCA loadings, on the other hand, ranked invertivores and grazers as the most responsive groups, while corallivores and planktivores had lesser and nearly equal rankings, and predators and scrapers 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.
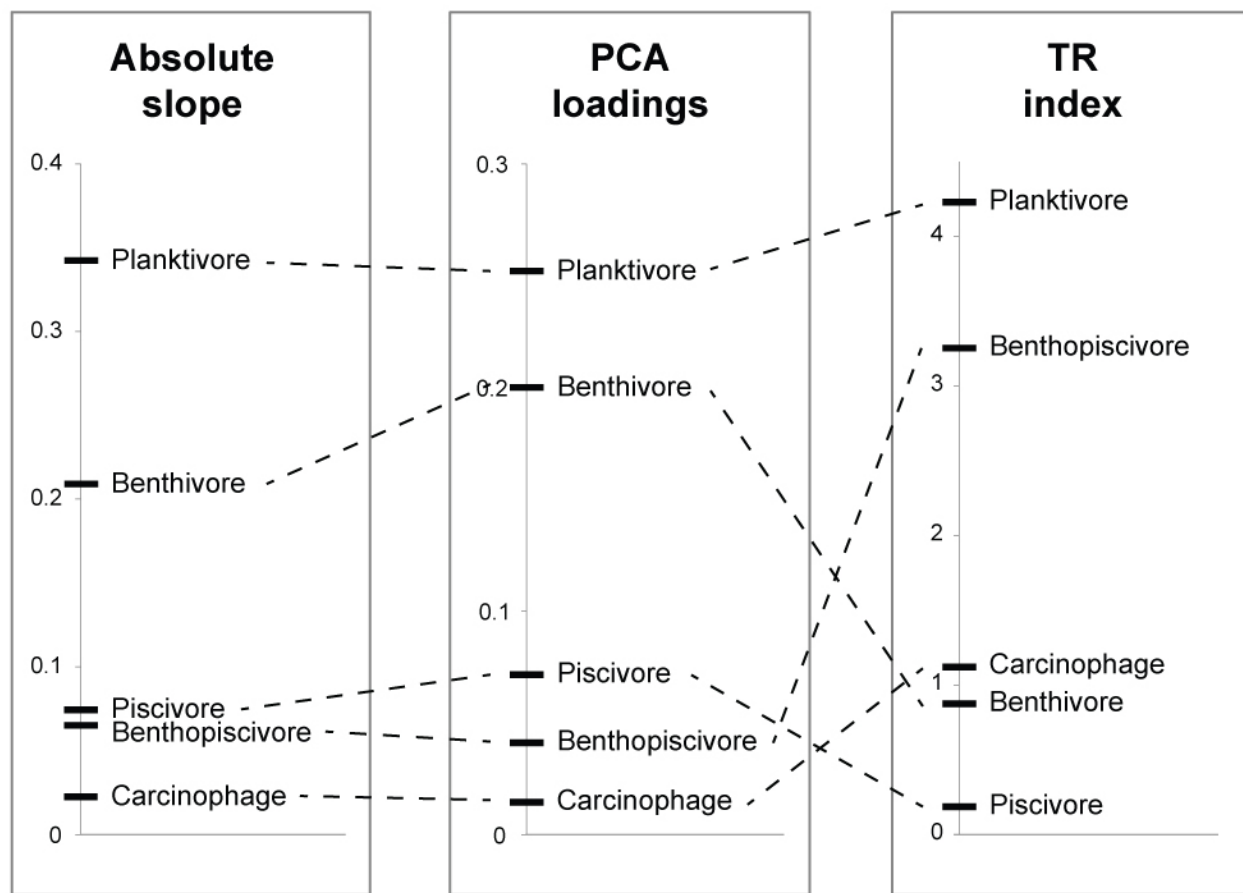
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240   **Fig. 3** Comparison of slope, PCA loadings, and the TR index for assessing the contributions of
241   reef-fish trait groups to community responses following mass coral mortality due to coral-
242   bleaching.
243

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

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

Discussion

Our results draw attention to the danger of statistically examining trait dynamics without

considering interspecific differences, especially when communities are composed of few

dominant and many rare species. Here, we show that using different methods to examine the

same trends can lead to markedly different rankings of the trait groups that are most responsive to

environmental changes. Incorporating basic concepts like species dominance and response

consistency among trait group members lead to different results than standard community-level

methods and highlighted the importance of considering species-specific responses when

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 relive

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

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

361   followed.

362

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