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Matthew Mclean, David Mouillot, Sébastien Villéger, Nicholas a J Graham, Arnaud Auber

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Interspecific differences in environmental response blur trait dynamics in classic statistical analyses

McLean Matthew [1, 2, *] , Mouillot David [2], Villéger Sébastien [4], Graham Nicholas A. J. [3], Auber Arnaud [1]

[1] Unité Halieutique Manche Mer du Nord, IFREMER, Boulogne-sur-Mer, France
[2] MARBEC Université de Montpellier, CNRS, IFREMER, IRD, Montpellier Cedex, France
[3] Lancaster Environment Centre, Lancaster University Lancaster, UK

* Corresponding author : Matthew McLean, email address : mcleamj@gmail.com

Abstract :

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

Introduction

Using species' traits, defined as any bio-ecological feature influencing individual performance in a given environment (Violle et al. 2007), is widely advocated for understanding how biological communities respond to environmental change. This requires identifying which traits exhibit the greatest environmental responses and best characterize community dynamics (Lavorel and Garnier 2002; Mcgill et al. 2006; Suding et al. 2008; Dehling et al. 2016; Gross et al. 2017). More specifically, ranking the respective contributions of different traits to community responses can help identify the ecological mechanisms structuring communities (Weiher and Keddy 1995; Pollock et al. 2012; Fort et al. 2014; Sakschewski et al. 2016). For example, in a marine fish community, if all species increasing in abundance are related by high temperature preferences, we could likely conclude that changes in community structure are primarily driven by ocean warming, and that future increases in warm-adapted species are likely (Cheung et al. 2013). While this response-trait approach is recognized for providing clearer information for planning conservation and management efforts that are applicable across ecosystems and taxa (Díaz and Cabido 2001; Winemiller et al. 2015; Pecuchet et al. 2017), proper interpretations of trait responses are critical.

Currently, descriptive statistics like ordination analyses are used to rank the respective contributions of different traits to temporal and spatial community responses, i.e. which traits are most responsive to environmental changes in time and space (Peres-Neto et al. 2003; Pla et al. 2011; Legendre and Legendre 2012). In temporal dynamics, principal component analysis (PCA) is used to examine changes in a given community over time by examining the movement of the community along the main principal component axes, while the most responsive traits are inferred by ranking PCA loadings (Peres-Neto et al. 2003; Pla et al. 2011; Legendre and

Legendre 2012). Additionally, trait responsiveness can be inferred as the slope of the regression between trait abundance and time or an environmental gradient (Noordijk et al. 2010; Jamil et al. 2014). From a purely descriptive standpoint, these methods provide accurate assessments of the traits that explain the highest amount of variation in a dataset, and thus accurately identify the traits with the greatest contributions to community variation in a statistical context. However, using only such descriptive statistics can lead to misinterpretations of how traits respond to environmental changes.

While ordination or regression-based methods might accurately indicate which trait increased or decreased the most over time or space, this finding does not necessarily mean that this trait was the most responsive to environmental changes. For example, if a certain trait emerged as the most responsive because it had the greatest regression slope, this result could be due to a single dominant species while all other species with this trait were unaffected, thus questioning the unequivocal responsiveness of this group. For instance, 'piscivore' could be identified as the trait most impacted by an environmental disturbance, yet if only one dominant piscivore species decreased in abundance, while all remaining piscivores were unaffected we have little confidence that piscivores are actually affected by this disturbance. Even though, under the mass-ratio hypothesis, changes in the traits of the most abundant species should have the highest impact on ecosystem processes owning to their dominance, it does not imply that they are the most representative of how traits in general respond to changing environments (Grime 1998; Díaz et al. 2007; Mokany et al. 2008). Rather, other traits could be far more responsive to environmental changes, but simply less dominant in the community. Another problematic case arises when a particular trait is shared by only a few species. If these species increase or decrease synchronously in abundance just by chance, standard methods might indicate that the trait is highly responsive while actually being a random signal (Peres-Neto et al. 2017). Instead, when a

trait is shared by many similarly affected species, we have greater confidence that this trait contributes strongly to community responses, and is highly responsive to environmental change.

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

Materials and Methods

Trait group contributions to community responses

Here, 'trait' refers to any morphological, physiological or phenological feature related to organismal fitness (Violle et al. 2007). In this study, for simplicity, we considered trait groups (commonly referred to as functional groups), which are defined as groups of species with shared trait attributes (e.g., pelagic, demersal, piscivore, planktivore, schooling, diurnal, oviparous, etc.). Thus, groups were not chosen in order to combine species with similar responses, but rather were defined according to shared bio-ecological characteristics. This trait-based approach is commonly used to identify whether certain shared characteristics explain how species respond to environmental perturbations (Engelhard et al. 2011; McLean et al. 2018b). While considering groups is most relevant for categorical traits, it can be easily extended by grouping continuous traits, which is common in trait-based studies (Mouillot et al. 2014; D'agata et al. 2016).

However, it should be noted that the issues outlined above apply equally to community-weighted mean approaches, particularly because dominant species can drive changes in average trait values, masking the responses of other species with similar trait values.

Here, we developed a simple index to demonstrate the potential misinterpretations of using standard statistical methods that do not account for interspecific variation in environmental responses. However, it should be noted that this index is used purely for demonstrative purposes and is not proposed a solution for integrating interspecific differences into trait dynamics. This simple index, hereafter called the trait response (TR) index, ranks trait group contributions to temporal community dynamics. This index thus considers changes in community structure over time and identifies the most responsive trait groups. This index has three complementary criteria:

i. The slope of the change in trait groups over time (i.e., Δ abundance or biomass time^{-1}).
ii. Kendall's coefficient of concordance, a measure of consistency among changes in trait group member's abundances (i.e., whether species within a given trait group display similar dynamics), ranging from 0 to 1 (Legendre 2005). When the coefficient is 1, all species display the same type of change; when the coefficient is 0, there is no consistency among species, and the dynamics of the corresponding trait group are essentially random. Kendall's coefficient is calculated by rank-ordering the abundances of each species across years, and consistency among species' abundance rankings within each group is computed via the mean and sum of squared deviations of the rankings (see Legendre 2005).
iii. The number of species whose temporal trends (increase vs. decrease in abundance) are the same as the overall group to which they belong, i.e., if the overall trait group decreased in abundance, the number of species in this group that decreased in abundance. This

component first adds a probabilistic aspect, reinforcing that higher numbers of species with consistent responses reduce the likelihood that trait group dynamics are due to chance alone. Secondly, it complements Kendall's concordance, which can be equal for groups with different numbers of species. For example, groups consisting of singletons or doubletons could show very high slopes and have 100% response consistency, however, having only 1 to 2 species limits our confidence that this group is truly responsive, whereas a higher number of species showing consistent responses increases our confidence.

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

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

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

Simulated case study

To qualitatively demonstrate the problems outlined in the introduction, we first created artificial datasets of species' abundances and traits, where we considered changes in the abundance of ten species comprising four trait groups over four years (note that some species belonged to more than one group) (Fig. 1a-d). For this theoretical example, species abundances were specifically (i.e., non-randomly) chosen to highlight the case of a right-skewed community distribution due to many rare and one dominant species, and the potential impact this can have on analytical interpretations. Thus we allocated large decreasing abundances to a single species, and assigned lower abundances to all other species. We furthermore adjusted species' abundances so that three of the trait groups had low response consistency among species (groups 1, 3, and 4), while one trait group had high consistency (group 2). Temporal dynamics of the trait groups (Fig. 1e) were first calculated using the two standard methods – the slope of the abundance of each trait group over time and the PCA loadings of each group. The TR index was then calculated and trait group contribution rankings were compared across the three methods.

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

We next examined coral-reef fish dynamics following a mass coral bleaching event, specifically examining which trait groups were most impacted by coral mortality. The Seychelles Islands experienced wide-spread coral mortality following severe bleaching during the 1998 El Niño event, which led to substantial changes in benthic structure and reef fish community composition (Graham et al. 2015). Fish abundance data were collected at 21 sites around the Seychelles Islands using underwater visual census (UVC) in both 1994 (pre-bleaching) and 2005 (post-

bleaching). Abundance data were collected for 129 species, which were assigned to six trait groups according to species' main diets: predators, invertivores, planktivores, grazing herbivores (grazers), scraping herbivores (scrapers), and corallivores (Graham et al. 2015). Because dominant species can bias group dynamics (as outlined above), all species abundances were log10(x+1) transformed before analyses. Standard data transformations such as log and Hellinger can strongly alleviate the influence of dominant species; however, data transformations cannot entirely resolve the issues outlined in the introduction, as species' abundances often vary by several orders of magnitude. The TR index was then calculated and trait group rankings were compared with the rankings from the absolute value of slope and PCA loadings.

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

We next applied the TR index to long-term fish community data in the southern North Sea, again examining which diet groups were most responsive to environmental changes through time. The southern North Sea has experienced significant community change in the last thirty years due to sea surface warming, with marked increases in warm-adapted species (Dulvy et al. 2008; Engelhard et al. 2011; Cheung et al. 2013). Fish abundance data have been collected annually since 1983 across the entire North Sea during the fisheries monitoring campaign the International Bottom Trawl Survey (Verin 1992). Here we included data for the southern North Sea (area approximately south of the 50-m depth contour; Pecuchet et al. 2017; McLean et al. 2018a) ranging from 1983 to 2015 for 110 species. Species were assigned to five trait groups according to their main diets: piscivores, benthopiscivores, carcinophages (crab-eating), benthivores, and planktivores. All species abundances were log10(x+1) transformed before analyses. We then calculated and compared the TR trait group rankings against rankings of the absolute value of slope and PCA loadings.

Results

Simulated case study

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

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

Long-term changes in North Sea fish communities

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

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.

While rarely discussed in current literature, ignoring the potential impacts of individual species responses, notably dominant species and species with inconsistent dynamics, can greatly bias statistical results and remains a prevalent issue in trait-based studies. Numerous studies examining temporal changes in communities' trait structures use methods such as PCA, redundancy analysis (RDA), or RLQ analysis (co-inertia analysis of environmental (R), species (L), and trait (Q) matrices), which are all heavily influenced by dominant species. Additionally, while we examined trait groups according to categorical traits, applying such methods to community-weighted mean trait values rather than trait groups does not relieve the issue, as major changes in trait dominance can be entirely driven by single species (Bello et al. 2007, 2012; Nickerson et al. 2018). While recent approaches have been developed to identify the contribution of different species to changes in a single community-weighted mean trait (e.g., temperature preference) (Princé and Zuckerberg 2015; Gaüzère et al. 2019), this issue remains unresolved for multi-trait approaches. Here, for simplicity, we examined changes in multiple trait groups within the single trait 'diet,' however, integrating multiple traits is necessary to fully

characterize community responses to environmental change (Lefcheck et al. 2015). Studies examining fish community dynamics generally integrate several traits such as habitat use, diet, body size, and reproductive mode (Frainer et al. 2017; Pecuchet et al. 2018; McLean et al. 2019). Identifying the traits that are most responsive to environmental changes (rather than identifying the species that contribute most to changes in a single trait) in such multi-trait studies is substantially more difficult, as multi-trait dynamics are clearly blurred by interspecific differences.

Furthermore, choosing and assigning traits to different species can have a major impact on results depending on the dominance and dynamics of the species. For example, when a dominant species is both a planktivore and a piscivore depending on ontogeny and resource availability, if the species is classified as a piscivore and has major changes in abundance, the overall conclusion will be that piscivores are heavily impacted by disturbance, even though this result was driven by a single opportunistic species. While seemingly intuitive, such issues remain widespread in trait-based studies and their potential consequences are rarely considered.

A central goal of trait-based ecology is to understand how organisms respond to environmental gradients, notably to anticipate future biodiversity changes (Keddy 1992; Weiher and Keddy 1995; Mcgill et al. 2006; Winemiller et al. 2015). As human impacts continue to change the global environment, understanding how different trait groups will respond is critical to planning how we will adapt conservation and management efforts to maintain ecosystem services (Vitousek et al. 1997; Hulme et al. 1999; Edwards and Richardson 2004; Thuiller et al. 2006; Poloczanska et al. 2013). As the power of trait-based ecology lies in understanding fundamental trait-environment relationships, we must consider ecological implications, like species-specific responses, to a greater extent in statistical methods. The greatest potential danger lies in misidentifying traits that are most responsive to environmental changes, especially for

resource management. For instance, in the artificial example, standard methods identified trait group #4 as the most responsive, which could lead to the conclusion that group #4 is the most characteristic of the community response. Thus, resource managers might mistakenly believe that environmental changes most prominently impact communities through decreases in species in group #4, when in fact decreases in species in group #2 are much more representative. By misidentifying trait-environment relationships driven by dominant species, resource managers could be ill-prepared for sudden changes in community structure driven by rare species.

In our reef fish example, an ecosystem at the forefront of climatic disturbance (Graham et al. 2015; Hughes et al. 2018), standard statistical methods (i.e., PCA) could support the conclusion that invertivores are the most responsive trophic group to coral bleaching, leading to potential misallocation of resources, when in reality corallivores are much more responsive and present a more critical management target. In the southern North Sea, an ecosystem highly impacted by climate warming (Dulvy et al. 2008; Engelhard et al. 2011; McLean et al. 2018a), standard methods would conclude that benthopiscivorous species have been relatively unimportant to community dynamics through time and are thus unresponsive to sea surface warming, when in reality this group has shown consistent, positive responses. These examples highlight how our basic understanding of community responses to climate change can be compromised if we fail to consider the interspecific differences behind trait dynamics.

As our primary objective in this concept paper was not to develop a new method for examining trait dynamics, but to highlight potential issues arising from standard methods, we acknowledge that the index used here is both basic and imperfect, and alternatives with other ecological criteria and different mathematical structures are feasible. For example, while our index was based on consistency among group members using Kendall's coefficient of concordance, this approach cannot account for competition among species within groups, or

functional replacement by unaffected species within the same group (i.e., via functional redundancy). However, we reconcile that groups containing species that show inconsistent environmental responses (i.e., some decrease while others increase) due to competitive release or functional replacement are likely not the most environmentally-responsive groups given that some species suffer while others benefit. Rather, other traits may better explain why species increased or decreased in abundance, and groups where nearly all species are similarly affected are likely more responsive. Kendall's concordance may also not be well adapted for hyper-diverse regions because too many species packed within few groups could mask the responses of highly impacted group members. Moreover, we also suggest examining each of the three indicators composing the TR index, as similar TR values among groups can hide different response patterns (e.g., small changes in abundance with high Kendall's concordance and vice versa). We therefore encourage others to propose additional ecological criteria relevant to examining trait dynamics and to develop alternative methods that build on the concepts presented here. Furthermore, with the goal of accurately identifying trait group responses to environmental change, additional approaches focusing on the underlying mechanisms of trait responses will greatly increase our understanding of trait-environment relationships. Laboratory studies examining how different trait groups, and their constituent species, respond to environmental variation like sea-surface warming can more concretely determine which traits are truly most sensitive to environmental changes, and identify the physiological characteristics linking these traits (Ospina and Mora 2004; Sandblom et al. 2014; Verberk et al. 2016; Messmer et al. 2017). Such understanding will be critical for anticipating the ecological impacts of global environmental change.

The examples in this concept paper bring to light a specific case in prioritizing trait group responsiveness, but also draw attention to the larger issue of framing data analyses and

interpretations in ecological contexts. While many powerful tools are readily available to contemporary ecologists, the corresponding results are only as good as the interpretations they permit. As trait-based ecology continues to expand, it is important that we consider the ecological contexts of methods and results in order to generate trait-environmental relationships that accurately reflect community dynamics, a critical step for better understanding ecosystem functioning.

Compliance with Ethical Standards

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

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Figures

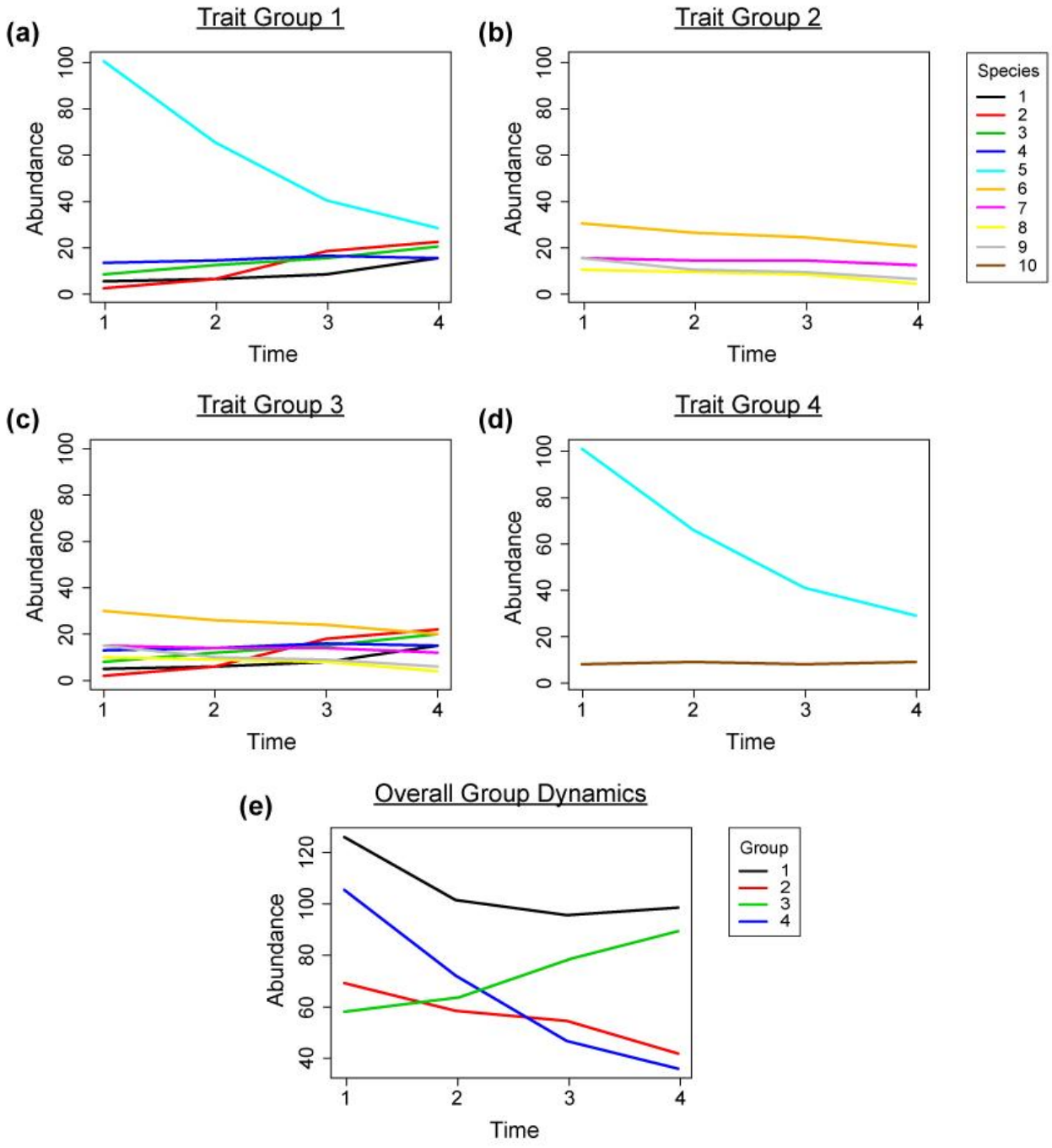

Fig. 1 Temporal dynamics of ten artificial species belonging to four different trait groups **a**-**d**, and the resulting dynamics of the trait groups themselves **e**. Artificial data were created to highlight the case where a single dominant species drives trait group dynamics (species #5), and where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

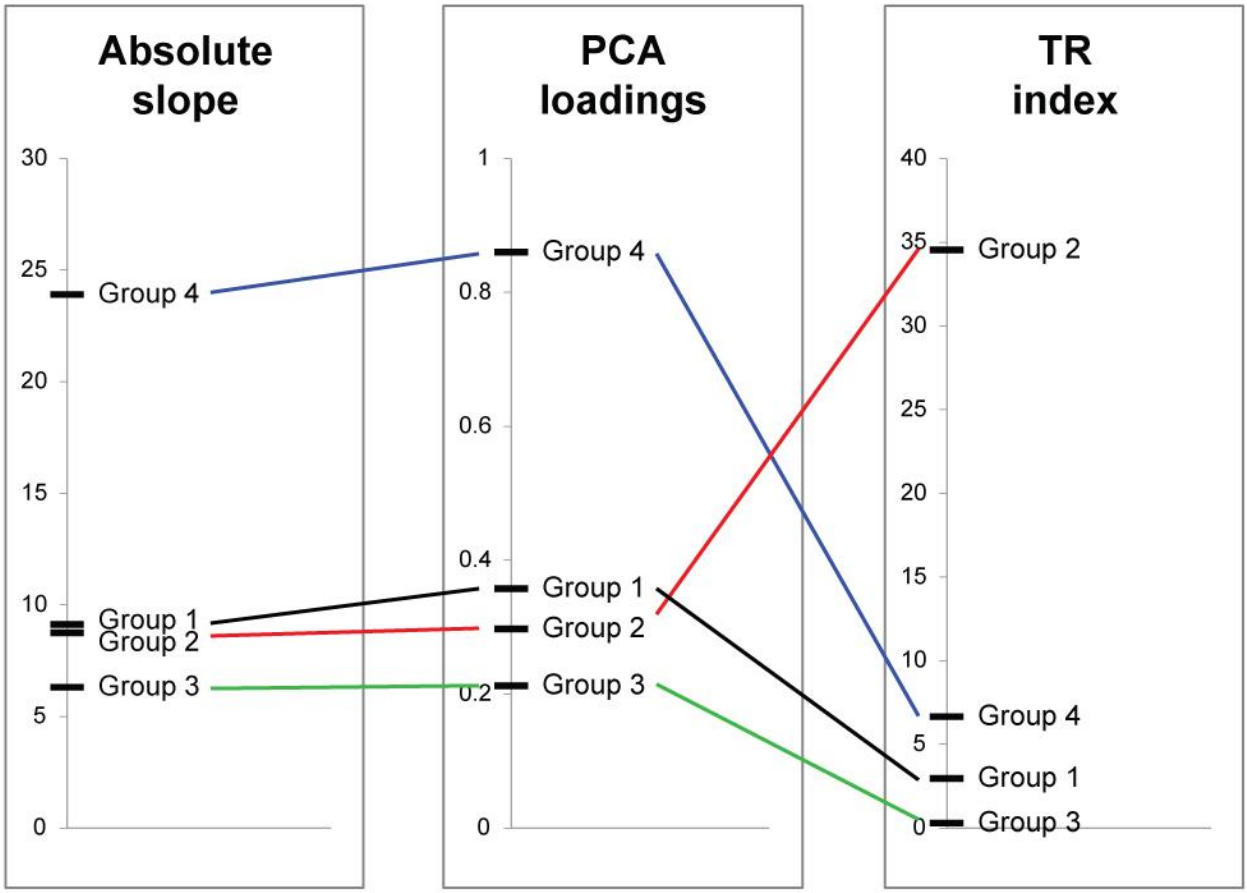

Fig. 2 Comparison of slope, PCA loadings, and the TR index for assessing the contributions of individual trait groups to the temporal responses of an artificial community of ten species comprising four trait groups.

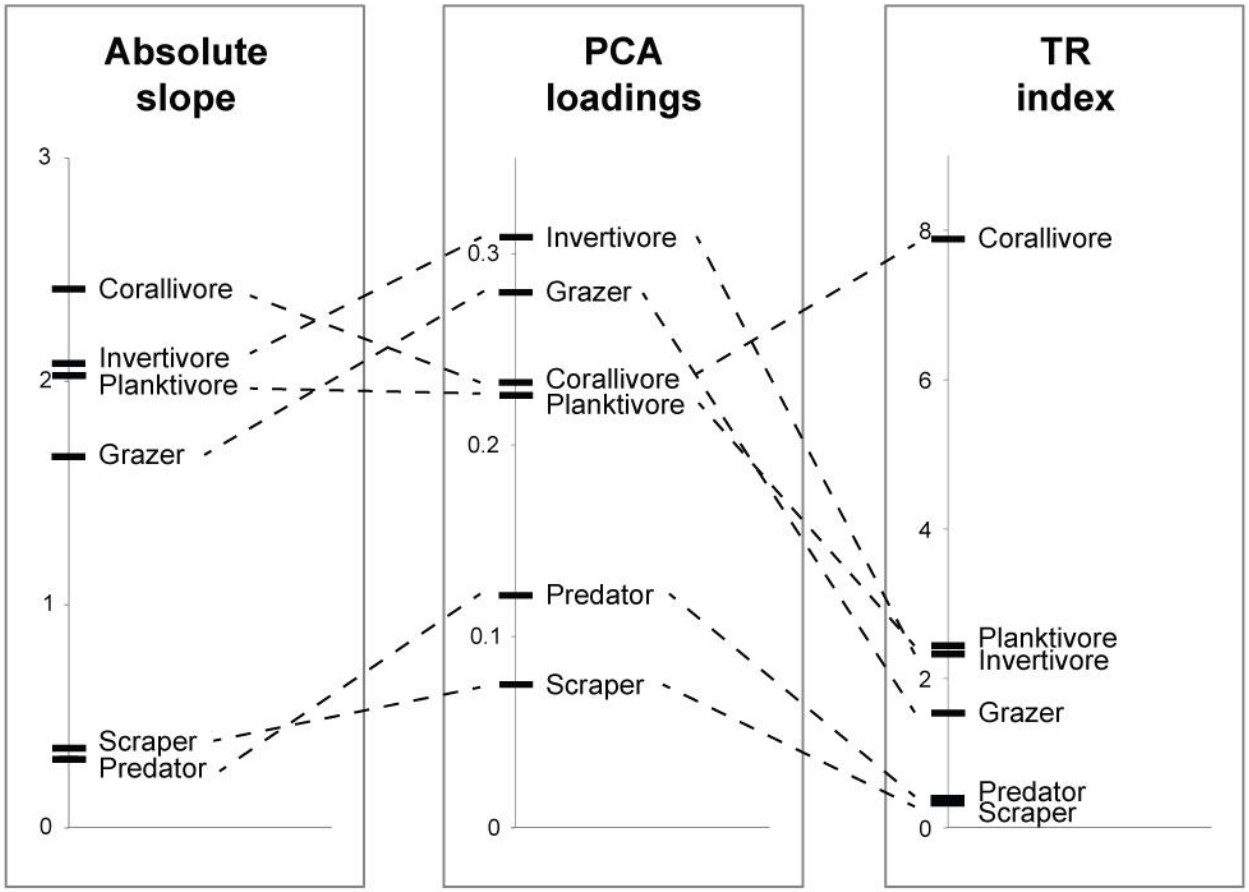

Fig. 3 Comparison of slope, PCA loadings, and the TR index for assessing the contributions of reef-fish trait groups to community responses following mass coral mortality due to coral-bleaching.

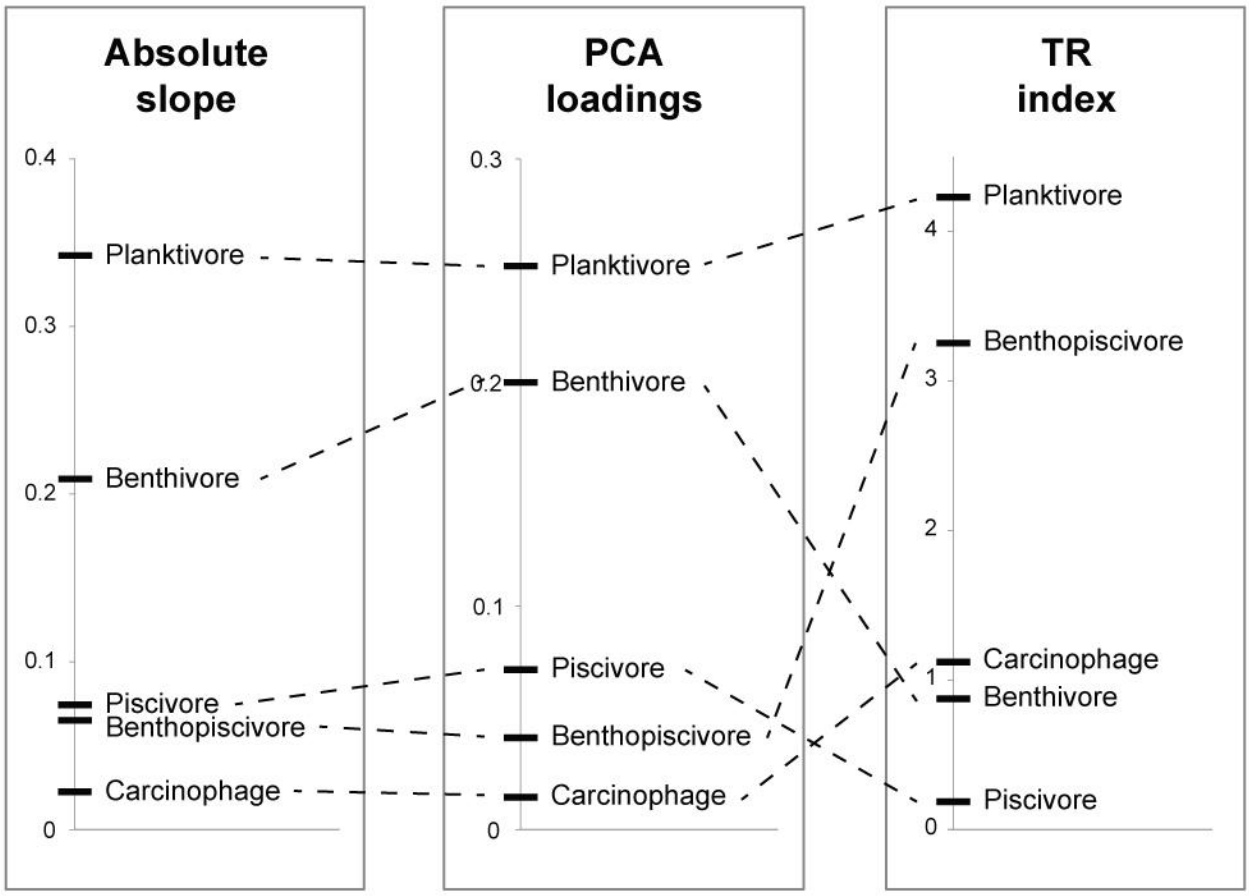

Fig. 4 Comparison of slope, PCA loadings, and the TR index for assessing the contributions of trait groups to long-term community responses in the outhern North Sea.