How to measure response diversity

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CRediT Author Contribution Statement| SRP-JR: Conceptualisation, Software, Formal analysis, Funding acquisition, Validation, Investigation, Visualisation, Methodology, Writing – original draft. **OLP:** Conceptualisation, Data curation, Software, Validation, Methodology, Writing – reviewing and editing. **TS:** Conceptualisation, Methodology, Writing – reviewing and editing. **DWA:** Conceptualisation, Software, Formal Analysis, Methodology, Writing – reviewing and editing.

Running title: How to measure response diversity

Keywords: diversity-stability debate; functional diversity; resilience; functional trait; asynchrony; environmental change; temporal variability; functional response; insurance hypothesis; nonlinear responses.

Article type: Synthesis

Words: Abstract 198 words; main text 4,765 words; boxes 1,009 words.

References: 134 references.

Display items: 4 figures (+1 in Box 2); 0 tables; 2 text boxes.

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Abstract

Taxonomic diversity metrics are, at best, proxies for the inter- and intraspecific trait differences that mechanistically underlie the insurance effect of biodiversity—that diversity enhances and stabilises aggregate ecosystem properties. In theory, variation in functional (*e.g.*, biomass) responses to environmental change can buffer and maintain ecosystem functioning. This variation, termed *response diversity*, is therefore a potentially critical determinant of ecological stability. However, response diversity has yet to be widely quantified, possibly due to difficulties in its measurement. Even when it has been measured, approaches have varied. Here, we review methods for measuring response diversity and propose a methodological framework for quantifying response diversity from experimental or observational data, which can be practically applied in lab and field settings across a range of taxa. Our approach, which is based on environment-dependent functional responses to any biotic or abiotic environmental variable, is conceptually simple and robust to any form of environmental response, including nonlinear responses. By capturing even subtle inter- or intraspecific variation in environmental responses, and environment-dependencies in response diversity, we hope this framework will motivate tests of the diversity-stability relationship from a new perspective, and provide an approach for mapping, monitoring, and protecting this critical element of biodiversity.

Introduction

Ecological stability has been a core focus of ecology since the 1950s when interest in the relationship between diversity and stability first arose (McCann 2000). Ecological stability is a multidimensional concept encompassing a range of metrics for measuring resistance to and recovery from disturbance, and variability in time and space (Pimm 1984; Donohue *et al.* 2013). Early observations suggested that more diverse communities are more stable in their ability to resist invasions or in the magnitude of their fluctuations (Odum 1953; MacArthur 1955; Elton 1958). Using randomly structured model communities, May (1973) then demonstrated that diversity *per se* did not increase stability (*i.e.*, did not dampen population fluctuations), but rather decreased it (see also Pimm & Lawton 1978; Yodzis 1981). Though debate continues (Jacquet *et al.* 2016; Pennekamp *et al.* 2018), subsequent developments (*e.g.*, McCann *et al.* 1998; Kondoh 2003; Ives & Carpenter 2007) have led to the consensus that in more complex models (that include for example, variable environments, interaction strengths, or behaviours), species-rich systems will exhibit more stable (less variable) aggregate ecosystem properties compared to species-poor systems (Ives *et al.* 1999). This is because declines in one species' abundance or performance—that is, any aspect of an organism's higher- or lower-level functional attributes (traits) that contributes to individual fitness or higher-level (ecosystem) functioning (Hooper *et al.* 2005)—will be offset by neutral or positive responses of other species or phenotypes (reviewed by Loreau *et al.* 2021). Together, these ideas encapsulate the insurance effect of biodiversity (Yachi & Loreau 1999)—that biodiversity both enhances and stabilises ecosystem functioning. However, despite biodiversity being only the "*passive recipient*" through which underlying ecological mechanisms drive stability (McCann 2000; Shade 2017), attempts to find a general and empirically quantifiable dimension of biodiversity that reliably predicts stability across contexts have had limited success. Various mechanisms giving rise to the insurance effect have been proposed, including: variable interaction strengths (*e.g.*, Yodzis 1981; McCann *et al.* 1998) or mixtures of interaction types (*e.g.*, Mougi & Kondoh 2012; Hammill *et al.* 2015); food web nestedness (*e.g.*, Thebault & Fontaine 2010); trophic flexibility and food web rewiring (*e.g.*, Kondoh 2003); dominant, rare, or otherwise key species (*e.g.*, Walker *et al.* 1999; Sasaki & Lauenroth 2011; Arnoldi *et al.* 2019; Ross *et al.* 2022); and asynchronous or compensatory dynamics (Gonzalez & Loreau 2009; Wang *et al.* 2021) in time (*e.g.*, Craven *et al.* 2018; Sasaki *et al.* 2019) or space (*e.g.*, Loreau *et al.* 2003; Wang & Loreau 2016). Recently, the concept of *response diversity* has also emerged as a potentially key, yet under-explored driver of stability (Pennekamp *et al.* 2018; Kahiluoto *et al.* 2019; Sasaki *et al.* 2019).

Response diversity characterises the range of responses to the environment displayed among members (e.g., individuals, species) of a focal group such as a population, guild, or community (Elmqvist *et al.* 2003; Nyström 2006; Mori *et al.* 2013). The concept was co-opted from elsewhere in

the biological sciences, where response diversity describes, for example, the variation in tumour responses to radiation therapy (Hlatky *et al.* 1994) or the range of cellular reactions to stimuli in the brain (Burrows *et al.* 1997). In ecology, Ives *et al.* (1999) posited that differences in how species respond to environmental change (that is, response diversity) may explain species diversity's stabilising effect on community stability. In a later study, Ives & Carpenter (2007) found that, in a model of randomly structured competitive communities, response diversity's stabilising effect on communities negated the destabilising effects of interspecific interactions. The authors conclude that species-environment relationships were more important for stability than were interspecific interactions (Ives & Carpenter 2007). Interspecific variation in species-environment relationships is critical for the maintenance of diversity in variable environments (Chesson 2000) and species-rich systems are thus anticipated to exhibit a wider diversity of species-environment interactions compared to species-poor systems (Vogel *et al.* 2019). This response diversity may, in turn, support a variety of stabilising mechanisms acting on the aggregate properties of communities and ecosystems. For example, response diversity may be the ecological mechanism underpinning many of the statistical explanations of the diversity-stability relationship, such as the portfolio effect (Tilman *et al.* 1998; Loreau 2010; Loreau *et al.* 2021). Moreover, response diversity can promote asynchrony in species' biomass or abundance through time (Sasaki *et al.* 2019) and species-specific tolerance to environmental conditions may be partly responsible for temporal and functional complementarity among species (Petchey 2003; Loreau & de Mazancourt 2013). Indeed, asynchrony may often be an outcome of response diversity (*e.g.*, Sasaki *et al.* 2019), suggesting that the often-observed stabilising effect of asynchrony on aggregate community or ecosystem properties (*e.g.*, Morin *et al.* 2014; Hector *et al.* 2015), may in fact be a by-product of underlying differences in species-environment relationships. It is thus beneficial to measure response diversity directly instead of (or as well as) asynchrony, since response diversity may capture properties of underlying species-environment relationships that do not manifest as asynchrony of biomass (or other functional attributes) through time. Further, given the challenge of statistically separating asynchrony among populations from asynchrony in species-environment responses (de Mazancourt *et al.* 2013), it may be conceptually and empirically simpler to focus efforts on the ultimate rather than proximate causal mechanism: response diversity.

There are still relatively few empirical studies that explicitly measure response diversity. Though we recognise that many studies may measure response diversity without labelling it such, a systematic review of the literature returned 47 ecology papers that empirically measured response diversity (see Fig. 1). These empirical studies used various methods to measure response diversity. The majority (n = 28 studies, ~60%) measured response diversity using functional traits (see Box 1 for

discussion), where the diversity of response traits— that is, those traits that predict some aspect of how a species responds to the environment (Suding *et al.* 2008)—represents response diversity, measured using the functional dispersion [FDis] index (*e.g.*, Spasojevic *et al.* 2016; Hordley *et al.* 2021; Schnabel *et al.* 2021). Some studies measuring the dispersion of functional response traits explicitly do so after defining functional effect groups (Laliberté *et al.* 2010; Thornhill *et al.* 2018; Sasaki *et al.* 2019; Morel *et al.* 2020), producing a response diversity measure closely aligned to the Elmqvist *et al.* (2003) definition, which specifies that response diversity should be measured among species contributing to the same ecosystem function (though subsequent definitions relax this requirement; *e.g.*, Mori *et al.* 2013). Most empirical studies measuring response trait diversity do so for trees (*e.g.*, Craven *et al.* 2016; Altomare *et al.* 2021; Schnabel *et al.* 2021) and other groups of plants (*e.g.*, Mandle & Ticktin 2015; Döbert *et al.* 2017; Morel *et al.* 2020), or for freshwater or terrestrial invertebrates (*e.g.*, Mumme *et al.* 2015; Thornhill *et al.* 2018).

Another approach to measuring response diversity empirically is to define a species-specific interaction term in multi-species models of, for example, abundance as a function of the environment (n = 8 studies; Fig. 1). If the species-specific interaction term passes some significance or model selection threshold, then species are claimed to differ in their abundance ~ environment slopes; that is, they exhibit response diversity (Winfree & Kremen 2009). This approach to measuring response diversity has emerged primarily from the pollination literature (Winfree & Kremen 2009; Bartomeus *et al.* 2013; Cariveau *et al.* 2013; Stavert *et al.* 2017), but has been used elsewhere (Fauchald *et al.* 2011; Malyshev *et al.* 2016), and is based on the assumptions of linear regression models, meaning nonlinear responses are not captured. Another related but less common approach to measuring response diversity (n = 2 studies) is to measure some aspect of a population's performance, such as its intrinsic rate of increase (*e.g.*, McCann 2016) or biomass change in response to the environment, and take the range of performance-environment model slopes as a direct measure of response diversity. Leary & Petchey (2009) did this with four ciliate species by modelling their intrinsic rates of increase against temperature when in isolation, first determining species-specific environmental responses. They then assembled experimental communities with different combinations of these species, producing different levels of response diversity. Using observational time series of reef fish abundance, Thibaut *et al.* (2012) similarly quantified response diversity as the average correlation coefficient between pairwise combinations of species in terms of their intrinsic rates of increase as a function of the environment. These various methods for measuring response diversity have emerged independently, resulting in a disconnect among empirical response diversity studies, and a general methodological framework for measuring response diversity is lacking.

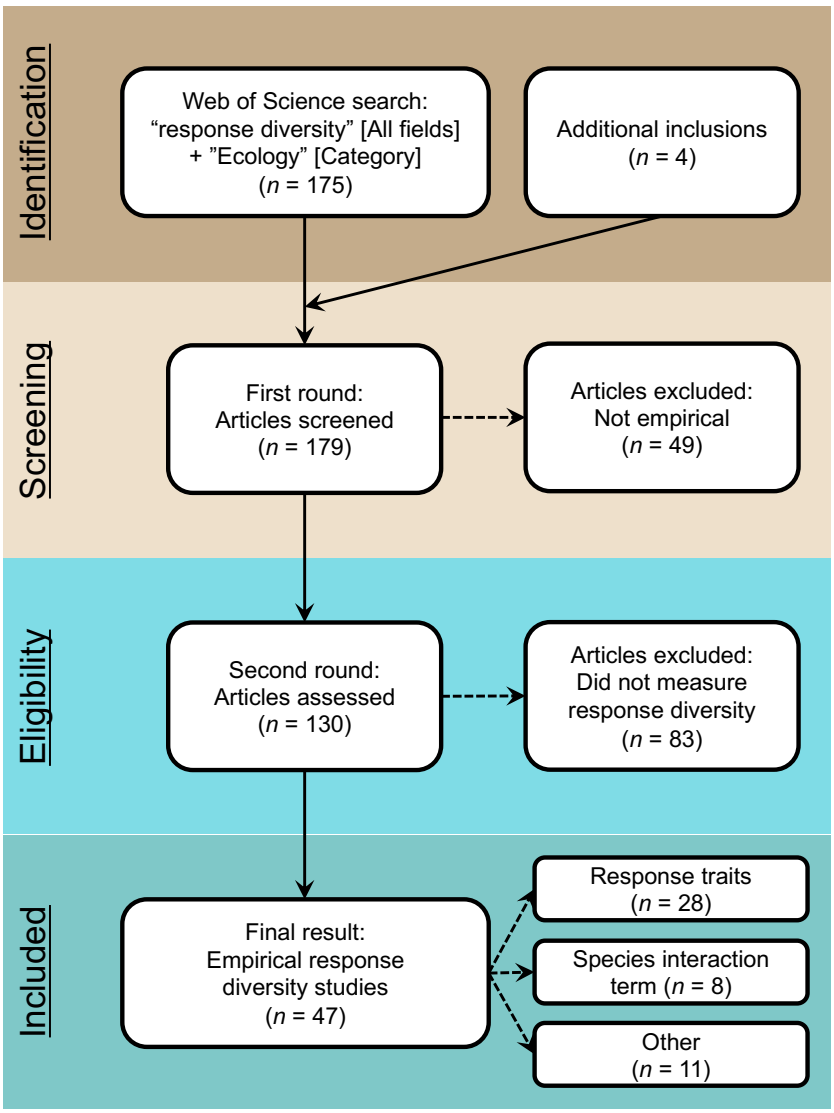

Figure 1. PRISMA diagram detailing the results of our systematic review. On 17 Dec 2021, we conducted a Web of Science search for "response diversity" in all fields within the "Ecology" Web of Science category. We supplemented the resulting 175 papers with four that we knew to be relevant but were not included in the initial results. We first excluded 49 articles that were not empirical studies (reviews, perspectives, *etc.*). Next, we screened the full-text articles and excluded 83 papers that did not measure response diversity (whether termed response diversity or not) based on the broad definition that response diversity should in some way characterise the range of species responses to environmental conditions. The resulting 47 empirical response diversity papers measured response diversity using various methods, the majority using functional response traits, followed by species-specific interaction terms in multi-species models of responses to the environment. We additionally searched using the term "response variation" which returned nine hits, of which eight were excluded and one was duplicate with our initial search. For consistency in categorisation and exclusion criteria, all screening was conducted by a single researcher (S.R.P-J.R.).

Measuring response diversity empirically

Here, we propose a framework for empirically measuring response diversity using a conceptually simple and empirically tractable approach that can be applied in observational and experimental settings in both the laboratory and field. We extend the models describing performance-environment relationships presented above to include any functional attribute that represents a species' functional response along a continuous gradient of abiotic or biotic environmental condition. In contrast to most previous studies of response diversity which focus on 'low-level' functional traits such as nitrogen content or specific leaf area (Box 1), our approach considers response diversity a 'high-level' trait of *per capita* growth rates for instance, tying it more directly to species performance. We discuss the strong potential for non-linearity in responses leading to environment-dependent response diversity, and the importance of divergent responses to environmental change in stabilising aggregate ecosystem properties. We also discuss the importance of assessing if the diversity of responses includes responses that differ in direction. We then demonstrate the ease with which response diversity can be measured and manipulated for use in empirical tests of the diversity-stability relationship.

We propose to extend the performance-environment models used elsewhere (Leary & Petchey 2009; Thibaut *et al.* 2012) into a generalisable framework for measuring response diversity. Despite rarely being used to date, this method is easily tractable in experimental and observational studies (Thibaut *et al.* 2012), provides a more direct measurement of how species respond to the environment than, for example, functional response traits (Box 1), and allows identification of key contributors to response diversity (Leary & Petchey 2009). In such models the response variable need not be intrinsic rate of increase, but could in fact be any relevant functional variable, such as biomass, abundance, or an ecosystem function to which the species contributes (Fig. 2). Similarly, the '*environment*' to which species are responding does not have to be an abiotic feature such as temperature; it can be any continuous biotic or abiotic condition. For example, one could model the responses along a land-use intensification gradient (*e.g.*, Winfree & Kremen 2009; Moore & Olden 2017; Stavert *et al.* 2017; Fig. 2b), or in response to the abundance of a predator, competitor, or the availability of a prey species (*e.g.*, Fauchald *et al.* 2011; Fig. 3). The latter approach, using biotic conditions as the environment to which a species responds, is conceptually similar to modelling the functional response (Holling 1966), which in turn may scale with abiotic conditions such as temperature (Daugaard *et al.* 2019; Sohlström *et al.* 2021). Similarly, modelling biomass change in response to a competitor is akin to concepts in coexistence theory such as negative-frequency dependent growth (*e.g.*, Armitage & Jones 2019) or invasion growth rate (Grainger *et al.* 2019).

From such models, we suggest measuring response diversity as the variation in the slope of a performance-environment function evaluated over the environmental gradient in question. Specifically, we suggest using Generalised Additive Models (GAMs) to fit performance-environment relationships individually for each species using smoothing parameters as appropriate (Fig. 2a-c), then taking the first derivatives of these models to estimate model slopes along the environmental axis (Fig. 2d-f). GAMs are free from many of the assumptions of linear regressions and can be used to evaluate both linear and nonlinear responses, or a mixture of the two (Hastie & Tibshirani 1987; see Github). Response diversity can then be measured as the variation in the distribution of these derivatives to capture the variation in species-specific environmental responses (Fig. 2g-i). In practice, this variation could be described using any suitable estimator, but here we use a two-dimensional measure.

First, we use a similarity-scaled measure of diversity introduced by Leinster & Cobbold (2012). Briefly, similarity-based diversity (Eq. 1 in Leinster & Cobbold 2012) is calculated based on pairwise Euclidean distances (that is, *dissimilarity*) in performance-environment relationships between all pairs of species in the community. The metric is rooted in Hill numbers, with an exponent (q) defining the relative weighting of richness and evenness (Leinster & Cobbold 2012). Here, we fix q at zero, to focus on species richness, though our measure of dissimilarity includes information on species relative abundances within the *S* x *S* similarity matrix. Thus, we can use this similarity-based diversity as a metric capturing information on both richness and similarity in species' responses (see Leinster & Cobbold 2012; Github). We chose this estimator since it has several desirable properties for describing response diversity: it cannot decrease with species additions; does not increase with additions of redundant species responses; and captures even subtle differences in the distribution of different responses within the overall range. Response diversity should therefore be lowest (1) when all species respond identically (Fig. 2g), and highest when species responses are as dissimilar as possible (the estimator converges to species richness as performance-environment slopes diverge to infinity and –infinity).

Critically, whether the first derivatives of performance-environment relationships span zero is a key indicator of the stabilising potential of response diversity under a given environmental condition. As such, we also isolate and measure this property of response diversity using the formula $\frac{\mathrm{range}(x_e) - \left||\max(x_e)| - |\min(x_e)|\right|}{\mathrm{range}(x_e)}$, where $\mathbf{x_e}$ represents the derivative of a performance-environment relationship for environmental condition ($\mathbf{e}$). If the range of first derivates does not span zero (*e.g.*, Fig. 2d,e), then all species respond in the same direction to the environment (albeit at varying magnitudes). In such cases, there is no response diversity along this sign-sensitive axis of species responses (the estimator is zero). In contrast, when first derivatives are perfectly symmetric around

zero, the value is one. Without interspecific interactions, even large differences in the magnitude of response (that is, the dimension of response diversity discussed above) cannot be stabilising (Ives *et al.* 1999; Mougi & Kondoh 2012). Conversely, when the range of first derivatives spans zero for a given environmental state (*e.g.*, Fig. 2f), species responses are diverging (at least one species is decreasing while another is increasing), which we expect *a priori* to be stabilising. Our estimator is largest (1) when $\min(x_e) = -\max(x_e)$. If observing stable aggregate ecosystem properties (*e.g.*, biomass) when the range of first derivatives does not span zero, this suggests response diversity is not the mechanism driving stability in that case. Together, our chosen similarity-based diversity measure and this sign-sensitive index make up the two core dimensions of response diversity of interest. The specific metrics we use here may not be ideal for all use cases. Further work should thus consider the need to develop suitable estimators of response diversity when those proposed fall short, including the possibility of uniting the two dimensions of response diversity discussed here into a single metric. That said, we demonstrate here the utility of these estimators for quantifying response diversity in a range of contexts (Figures 2 and 3), including applications to real data (Box 2).

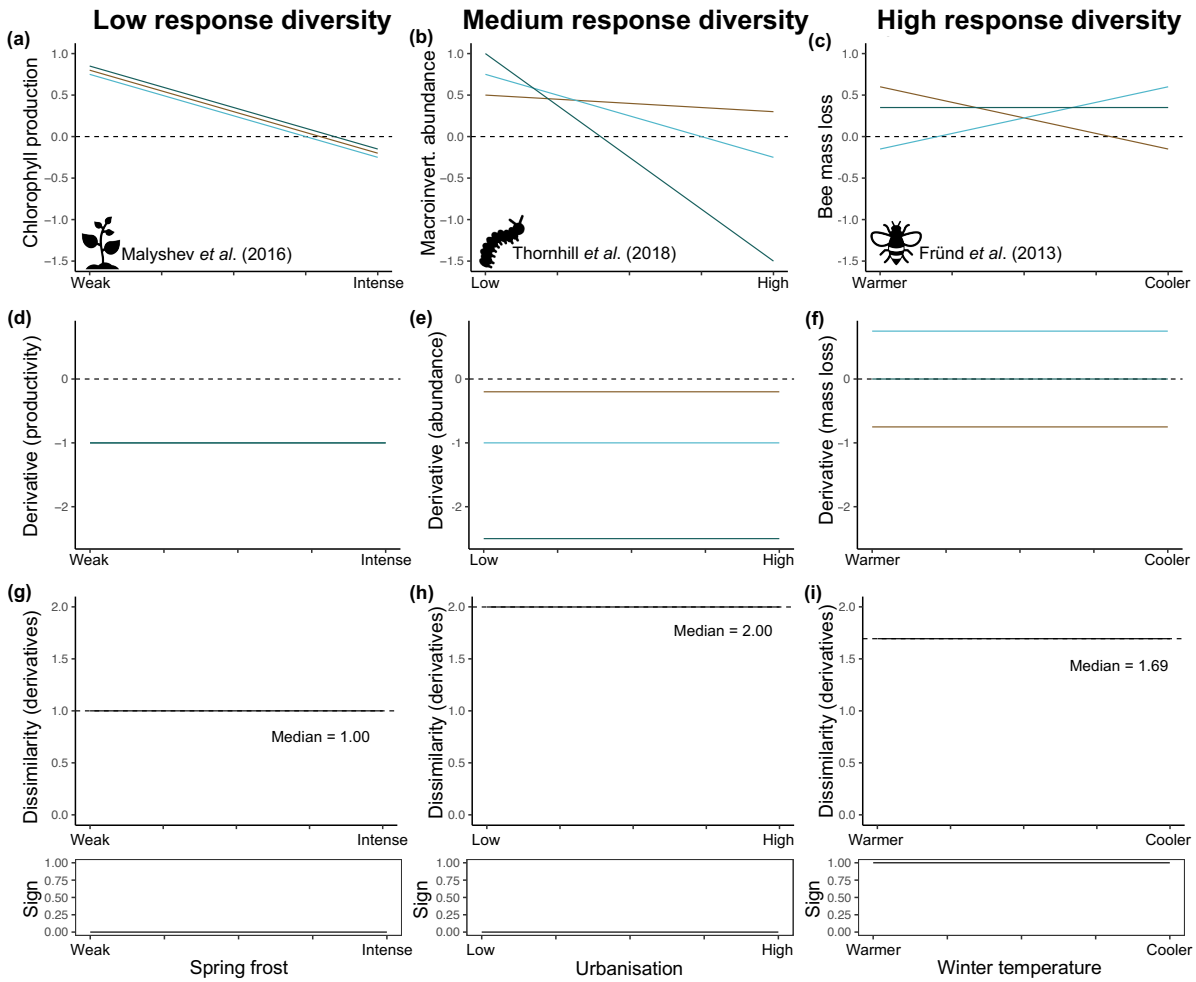

Figure 2. Measuring response diversity for linear species-environment relationships. We reimagined the original analyses of three studies, using standardised, simulated data to demonstrate how response diversity could be measured practically under our framework. (**a**) We propose a hypothetical case (based on Malyshev *et al.* 2016), where *Chlorophyll* production (which is often an indicator of biomass, particularly for aquatic plants) declines linearly across several species [coloured lines] of plants with spring frost intensity, with no difference among species in the slope of this decline. (**d**) We can calculate the first derivatives of these responses, which in this case would be identical for all species. (**g**) Then, we can measure response diversity using our proposed similarity-based diversity measure (see main text), and find it to be one (its lower bound), since all species respond identically to spring frost. Our sign-sensitive index is zero in this case, as the first derivatives do not span zero. (**b**) Next consider a case (based on Thornhill *et al.* 2018), where the abundance of several species of macroinvertebrates decline linearly, but at different magnitudes, along an urbanisation gradient. (**e**) Here, the first derivatives differ (as a result of the differing model slopes), resulting in a higher dissimilarity value (**h**). Again, the derivatives do not span zero, so the sign-sensitive index is zero. (**c**) Finally, we might be interested in the decline in mass of several bee species as a function of winter temperature (see Fründ *et al.* 2013). In this example, species responses to winter temperature diverge (one species increases, one decreases, and one is unaffected), but all such responses are linear, and the magnitude of the responses are not as extreme as in (**b**). (**f**) Thus, the first derivatives are less spread out than in (**e**), but span zero. (**i**) Accordingly, our dissimilarity value is lower than for (**h**), but in this case, our sign-sensitive index is at its maximum value, 1, across the entire range of winter temperature values (the derivatives span zero at any temperature). Dashed lines indicate zero in panels **a**–**f**, and the median value of the similarity-based diversity index (dissimilarity) along the X-axis in panels **g**–**l** (here, equivalent to any value along the X-axis since response diversity is constant).

Ecological responses to the environment are often nonlinear, necessitating a wide range of statistical tools for considering such responses (Fraterrigo & Rusak 2008; Ross *et al.* 2021b). When species' responses are nonlinear (*e.g.*, Leary & Petchey 2009), quantifying response diversity is not as simple as measuring the range of model slopes. However, the statistical framework we propose for measuring response diversity (that is, measuring variation in performance-environment first derivatives) is robust to nonlinearities such as species' functional responses to competition, predation, or resource availability (Fig. 3) or when tipping points are detected in empirical data (Berdugo *et al*. 2020). Figure 3 illustrates three such cases: one where the intrinsic rate of increase of flowering plant species responds nonlinearly but with low response diversity to total flowering plant abundance (Fig. 3a); one where seedling establishment responds to grazing pressure with higher response diversity among species (Fig. 3b); and one where trees respond nonlinearly to fire frequency, and differ in the form of this relationship (Fig. 3c)—our framework uses GAMs as they are robust even to cases where the form of the performance-environment relationship differs among species (Hastie & Tibshirani 1987; Fig. 3f,i). Where responses are nonlinear, the first derivatives of

performance-environment responses vary as a function of the environmental variable (along the X-axis in Figures 3d-f). In turn, this produces a measure of response diversity that also varies as a function of the environment (Fig. 3g-i). In cases where there is no need to treat response diversity as environment dependent, one could estimate a single response diversity value across the environmental axis using any summary statistic (see median response diversity in Figures 3g-i), though it may be appropriate to weight such a summary statistic by the distribution of the environmental variable. In linear cases, response diversity does not vary as a function of environment, so summary statistics are not required (Fig. 2).

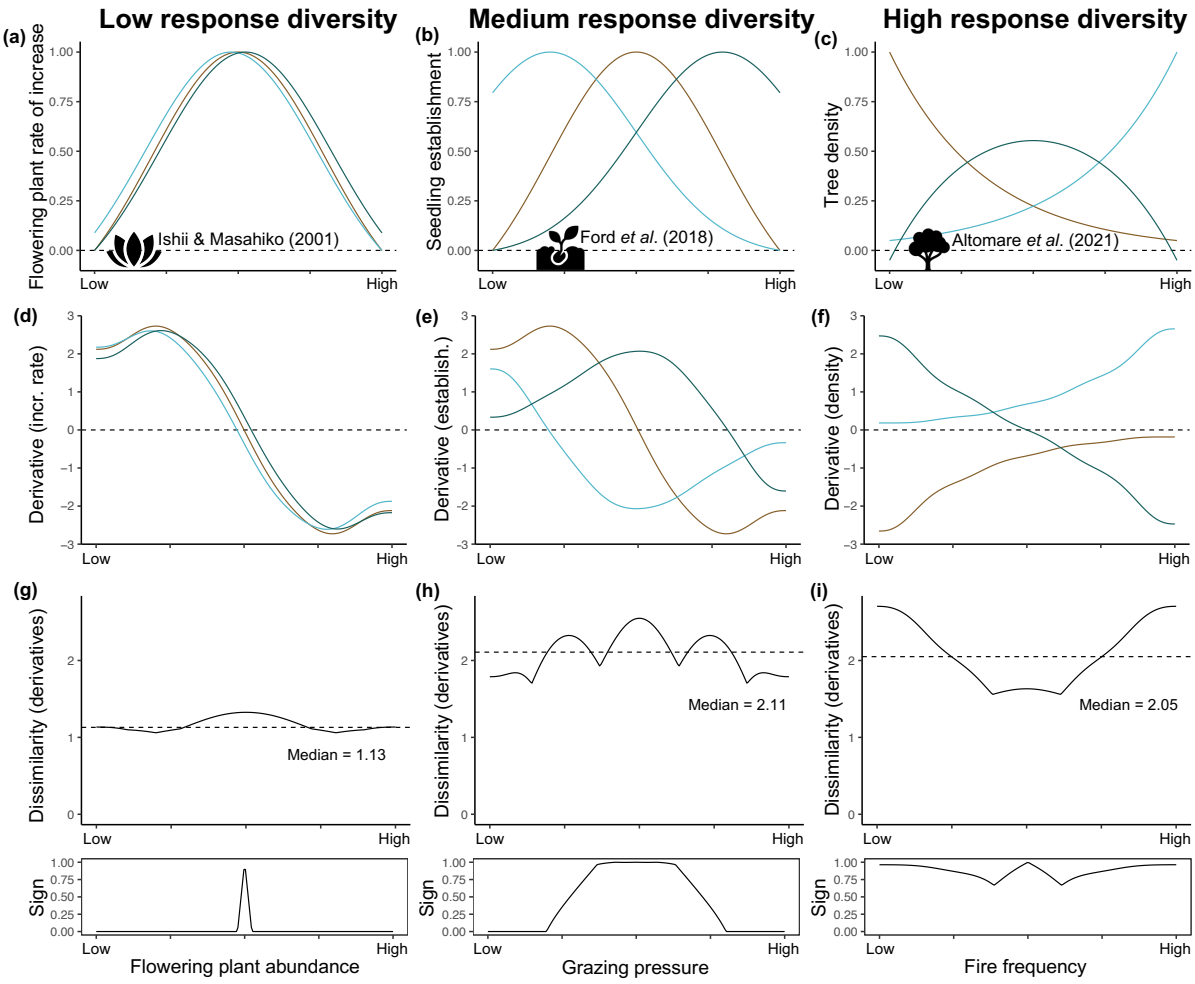

Figure 3. Measuring response diversity for nonlinear species-environment relationships. We reimagined the original analyses of three studies, using standardised, simulated data to demonstrate how response diversity could be measured practically under our framework. (**a**) We propose a hypothetical case (based on Ishii & Masahiko 2001), where flowering plant intrinsic rate of increase changes as a function of total flowering plant abundance. Here, responses may be nonlinear but similar in form, as competition is limiting at high abundance while pollinator visitations might be limiting where total flowering plant abundance is low (Ishii & Masahiko 2001; Reilly *et al.* 2020). (**d**) In this case, the first derivatives of the intrinsic rates of increase vary as a function of flowering plant abundance, but do not differ much among species. (**g**) This results in a dissimilarity value that

is close to its minimum (1) but varies a little with total flowering plant abundance. (**b**) Next consider a case (based on Ford *et al.* 2018), where seedling establishment of several plant species respond nonlinearly to grazing pressure. This might be the case if, for example, one species is a shade-tolerant understorey specialist [light blue] that does well when grazing pressure is low but not when high, while another species is a shade-intolerant disturbance specialist [dark blue] (Ford *et al.* 2018). (**e**) These divergent nonlinear responses produce a range of first derivatives that change as a function of grazing pressure, in turn producing (**g**) grazing pressure-dependent response diversity which is on, average, high in terms of dissimilarity, and is zero-spanning at intermediate grazing pressure. (**c**) Finally, consider a case (based on Altomare *et al.* 2021), where the density of several tree species responds nonlinearly to fire frequency with different functional forms. This might occur if some species are highly sensitive to burning [brown line] while others are disturbance specialists that require nutrient inputs from fire or reduced competition from dominant fire-sensitive species (Altomare *et al.* 2021). (**f**) Here, the first derivatives of tree density differ considerably and vary as a function of fire frequency, producing (**i**) generally high response diversity—in both dissimilarity and sign—that also varies with fire frequency. Here, response diversity is largest at low and high fire frequency (when specialists respond strongly) and is lowest at intermediate fire frequency. Dashed lines indicate zero in panels **a**–**f**, and the median value of response diversity along the X-axis in panels **g**–**i**.

By modelling individual species responses to environmental conditions with GAMs, this approach is conceptually similar to the species-specific interaction term described above (Winfree & Kremen 2009; Cariveau *et al.* 2013). However, the framework we describe provides a quantitative estimate of response diversity, identifying precisely the relevant differences in the form of species environmental responses (divergence, magnitude, *etc*.) that have the potential to drive ecological stability, and allowing consideration of response diversity as a function of the environment. This method is flexible enough to be used on traits, rates (first derivatives), or sensitivities of rates (second derivatives). We demonstrate cases taking first derivatives of traits before calculating response diversity (*e.g.*, Fig. 2b), thus producing *rates* from which we calculate response diversity (Fig. 2e). However, it is also possible to estimate derivatives of rates (*e.g.*, Fig. 3d and Box 2), producing a measure of sensitivity of those rates to environmental change, which can be ecologically meaningful when measured over environmental gradients (Shyu & Caswell 2014). However, study designs often estimate intrinsic rates of increase, for instance, under only two environmental contexts (*e.g.*, disturbed versus in-tact habitats). In such cases, it may be more meaningful to estimate response diversity based directly on the intrinsic rates of increase (rather than transforming them to second derivatives of abundance). Individual use cases will differ, so we suggest response diversity studies carefully consider whether response diversity should be measured based on traits, rates, or sensitivities, depending on available data and study goals. Practical users of response diversity can make use of the *mgcv* and *gratia* packages in *R* to fit GAMs and calculate derivatives, respectively

(Wood *et al.* 2016; Simpson 2021), and we provide *R* code to calculate response diversity for the simulated case studies from Figures 2 and 3 (available through Github).

Using the framework for measuring response diversity we present here, one can measure response diversity empirically in the laboratory or field. The key advantage of a conceptually simple and empirically tractable measure of response diversity is that it unlocks a range of questions that can be experimentally tested in controlled systems. For example, once the range of response trajectories among species—or individuals/populations for cases of intraspecific response diversity—is established, communities encompassing differing amounts of response diversity can be manually assembled (Leary & Petchey 2009; Baskett *et al.* 2014). This, in turn, allows testing a variety of questions with response diversity as the predictor variable, such as whether experimentally assembled communities with higher response diversity are more stable in terms of, for example, the temporal variability of total community biomass. In theory, performance-environment relationships can be established in isolation and then communities assembled from individual species responses. However, this approach neglects any interspecific interactions within multispecies communities. As such, it is likely more relevant to model species responses (individually, using species-specific GAMs; Github) within a multispecies community; thus allowing species-environment relationships to interact with species-species relationships as they would in nature (Ives & Carpenter 2007; Armitage & Jones 2020).

Observational time series can also contain rich information on, for instance, community dynamics or environmental responses (Ives *et al*. 2003; Ushio *et al*. 2018; Shoemaker *et al*. 2022). Though methods for inferring causality from time series are emerging (*e.g.*, *empirical dynamic modelling*, see Ushio *et al*. 2018; Ross *et al.* 2021b), such methods are often complex, and results must be interpreted carefully. In principle, our approach for measuring response diversity can also be applied to observational time series. For response diversity to be measurable in this way, time series should comprise higher-level traits as described above (*e.g.*, measuring intrinsic rather than realised rate of increase). Moreover, a high sampling resolution along environmental gradients is required to accurately differentiate between linear and nonlinear performance-environment relationships; longer or higher-resolution time series are better able to reveal nonlinearities in data, and response diversity experiments should be designed with sampling resolution in mind to sufficiently capture all possible forms of ecological responses. While the methods we describe here are useful for measuring multiple dimensions of stability from experimental or observational time series, response diversity could (perhaps more easily) also be measured over spatial gradients to assess spatial variation in the stability and synchrony of functional properties such as primary productivity among habitat patches (Loreau *et al.* 2003; Lamy *et al.* 2019; Wang *et al.* 2019, 2021).

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376 Future directions for empirical studies of response diversity

377 The framework for measuring response diversity introduced above is conceptually simple and
378 applicable across contexts. Using this approach, response diversity can be easily measured in
379 empirical settings (see Box 2 for reanalysis of data from Leary & Petchey 2009), and experimentally
380 manipulated, providing clear advantages over the functional trait approach dominant in the literature
381 (Box 1). Owing to its simplicity, our framework can be extended in several promising directions (Fig.
382 4).

383 First, rather than using response diversity solely as a predictor variable for estimating stability
384 responses, a system's response diversity to a given stressor could be measured as a function of
385 environmental change; that is, its magnitude at any given environmental state can be assessed and
386 compared to other treatments or replicates across any environmental ranges of interest. Such an
387 approach also permits quantification of response diversity to multiple environmental stressors (Fig.
388 4a), which often occur simultaneously (Garnier *et al.* 2017; Bowler *et al.* 2020). The change in
389 response diversity to one environmental condition as a function of a second then allows study of co-
390 tolerance to multiple stressors, and stress-induced community sensitivity (see Vinebrooke *et al.*
391 2004). It should also be possible to measure multivariate response diversity in the same ways that
392 multivariate functional trait diversity is measured (Petchey & Gaston 2006).

393 Second, given the multidimensionality of the ecological stability concept (Pimm 1984;
394 Donohue *et al.* 2013; Hillebrand *et al.* 2018), the predictive capacity of response diversity can be
395 tested as a driver of different stability dimensions (that is, response diversity as a predictor of
396 variability, resistance, resilience *etc.*; Fig. 4b). Another extension of this framework would consider
397 the relative importance of each species to community-level response diversity by, for example,
398 measuring the median dissimilarity in performance-environment model slopes between each species
399 and all others in the community (Fig. 4c). In this case, the species with the greatest dissimilarity from
400 the others should be the largest contributor to response diversity, and thus be that species whose
401 loss from the community should most greatly reduce response diversity, and hence stability (provided
402 the two are mechanistically linked). Such an approach complements studies considering the
403 contribution of individual species to ecological responses and stability (*e.g.*, Donohue *et al.* 2017;
404 White *et al.* 2020; Ross *et al.* 2021a, 2022), in turn, aiding progress towards targeted conservation
405 management decisions based on the quantifiable importance of individual taxa. Likewise, the
406 similarity-based diversity measure we used to estimate response diversity is based on hill numbers,
407 with an initial value of $q = 0$ indicating a focus on species richness. However, by increasing q to
408 higher values, it should be straightforward to also incorporate relative species abundances (Chao *et*

al. 2014), and hence the potential role of dominance or rarity (*e.g.*, Sasaki & Lauenroth 2011). Importantly, the subjects of a response diversity analysis need not be different species; individuals can also exhibit diversity in their response traits, further underscoring the importance of intraspecific variation in ecological responses to the environment (Barabás & D'Andrea 2016; Mimura *et al.* 2017; Ross *et al.* 2017; Herrando-pérez *et al.* 2019). Finally, if response diversity can be measured from observational time series, it should be conceptually straightforward to harness global datasets (*e.g.*, BioTIME; Dornelas *et al.* 2018) to unveil macroecological patterns and hotspots of ecological stability using response diversity (Capdevila *et al.* 2022; Fig. 4d).

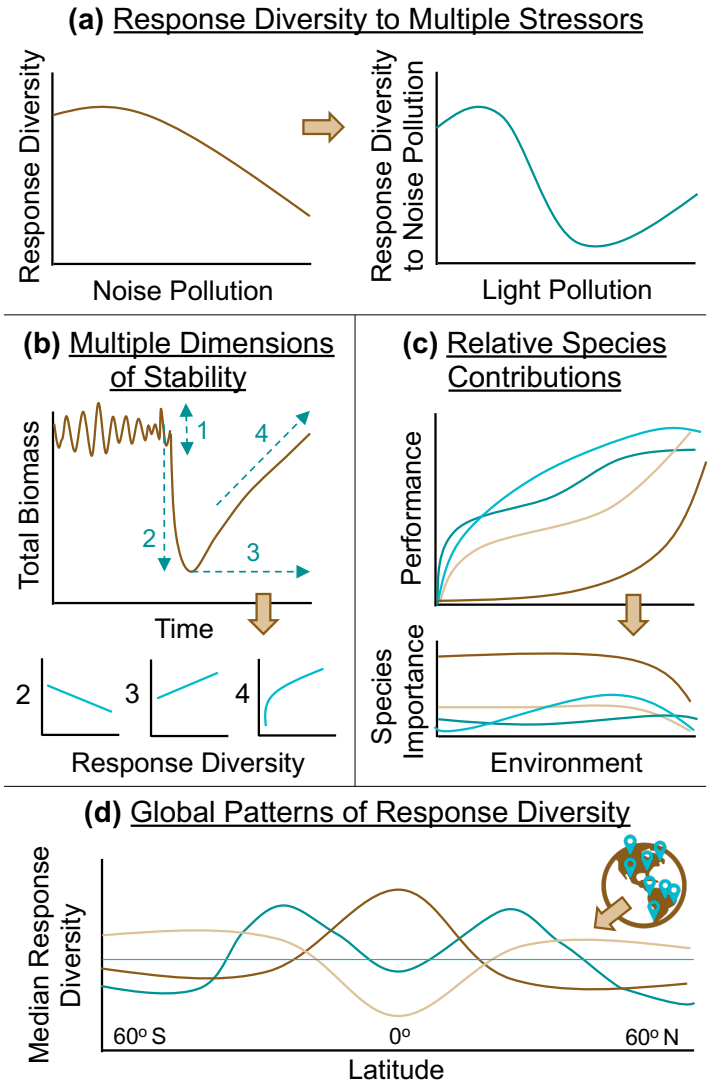


Figure 4. Future extensions to the response diversity framework. (**a**) After measuring response diversity to an environmental condition (*e.g.*, noise pollution), the change in response diversity to the first stressor could be modelled against a second stressor (*e.g.*, light pollution) to assess whether communities exhibit positive or negative co-tolerance to multiple stressors (Vinebrooke *et al.* 2004). It should then also be possible to develop multivariate response diversity metrics capable of predicting simultaneous responses to concurrent

environmental stressors. (**b**) Ecological stability is a multidimensional concept (Donohue *et al.* 2013); multiple stability metrics (*e.g.*, temporal variability [1], resistance [2], recovery time [3], and resilience [4]) can be calculated from a single response variable to a known disturbance. In such cases, response diversity can be used as a predictor of stability beyond just temporal variability, by extending tests of response diversity's predictive capacity to other dimensions of stability (here resistance, recovery time, and resilience), and response diversity may exhibit a different relationship with each stability dimension. (**c**) The relative contribution of species within a community to response diversity can be captured by considering how different each species is from the others under a given environmental condition. Here, we see the dark brown species is most different in its performance-environment relationship, resulting in the highest relative contribution (importance) of this species for response diversity. (**d**) With replicated global experiments or by exploiting global datasets of assemblage time series (*e.g.*, Dornelas *et al.* 2018), it should be possible to construct macroecological relationships for response diversity. For example, latitudinal response diversity gradients (coloured lines) should tell us something about whether certain communities or biomes may be 'hotspots' of resilience to environmental change.

That response diversity can be environment-dependent in cases where species respond nonlinearly to the environment has considerable implications for empirical studies of response diversity and for our understanding of ecological stability. Though threshold responses may be rare and/or difficult to detect in experiments (Hillebrand *et al.* 2020), nonlinear responses to many variables are common, such as Type II or III functional responses to prey availability (Holling 1966; Daugaard *et al.* 2019), or light or temperature response curves (*e.g.*, Peek *et al.* 2002; Payne *et al.* 2016). Nonlinear responses to the environment may result in environment-dependencies in species asynchrony (Shoemaker *et al.* 2022)—recently described using tail association methods (Ghosh *et al.* 2020a, 2020b; Walter *et al.* 2022)—in turn, producing environment-dependencies in ecosystem multifunctionality and stability (Morin *et al.* 2014; Sasaki *et al.* 2019). Environment-dependent response diversity may therefore explain inconsistencies in the reported effects of biodiversity on ecological stability across studies (Jacquet *et al.* 2016; Pennekamp *et al.* 2018). Importantly, the empirical framework we propose allows identification of the specific environmental conditions under which response diversity should or should not be stabilising. For a nonlinear environmental response, r(**e**), one can examine the values of **e** (the 'environment') for which the first derivatives of species-environment relationships, r'(e), including their confidence regions, span zero. In other words, our framework makes it conceptually and practically simple to identify *a priori* hypotheses regarding the stabilising effect of response diversity based on environmental conditions (Box 2). This should complement existing studies of the impact of environmental conditions on ecological stability (*e.g.*, Hillebrand *et al.* 2018; Ross *et al.* 2022). Moreover, in cases where response diversity varies as a function of the environment (that is, where species-environment relationships are nonlinear), it is

possible to manipulate response diversity without altering community composition. It might then be possible to identify response diversity as a stabilising mechanism by comparing the stability of aggregate ecosystem properties between communities of the same species under different (fixed) environmental contexts. Such an approach sidesteps the challenges associated with causal inference when comparing communities of different species; by controlling species identities, there are fewer potential confounding factors driving community-level responses (though environmental context is added as an extrinsic driver). For example, one could measure the diversity-stability relationship for a plant community with known performance responses to drought under drought and non-drought conditions to mechanistically consider how drought relate to stability. There is much still to learn about context-dependent ecological stability as it relates to nonlinear performance-environment relationships and environment-dependent response diversity, and we suggest this as a promising avenue of future work.

Since the observation that diversity alone is insufficient to explain the stabilising effect of species richness on aggregate ecosystem properties (May 1973; Ives *et al.* 1999), ecologists have been searching for a general mechanism explaining the insurance effect of biodiversity across contexts (Yachi & Loreau 1999). Here we proposed response diversity as a promising but understudied mechanism for predicting ecological responses to environmental conditions (Elmqvist *et al.* 2003; Nyström 2006; Mori *et al.* 2013). We found that most empirical studies of response diversity measure the diversity of functional response traits (*e.g.*, Laliberté *et al.* 2010; Morel *et al.* 2020). However, given the challenges associated with reliably producing functional response diversity estimates from trait data (Box 1), we suggest measuring response diversity as the variation in responses to environmental conditions (Leary & Petchey 2009; Thibaut *et al.* 2012)—unless using functional traits empirically demonstrated to encode sufficient information about responses to environmental change (*e.g.*, Kandlikar *et al.* 2022). The framework we propose herein provides a direct, empirically tractable, and conceptually simple measure of response diversity that should facilitate robust empirical tests of the diversity-stability relationship across taxa and environments. Such tests have the potential to identify the long sought-after mechanisms underpinning biodiversity's role in buffering ecosystems against environmental change.

Box 1. Response trait diversity: a reliable measure?

Functional diversity measures the extent of functional differences among species in a given community (Tilman 2001), and myriad functional diversity metrics are now used to estimate ecosystem functioning using functional traits, which represent a species' contribution to functioning (Díaz & Cabido 2001; Petchey & Gaston 2006; Cadotte *et al.* 2011). Given their effect on ecosystem

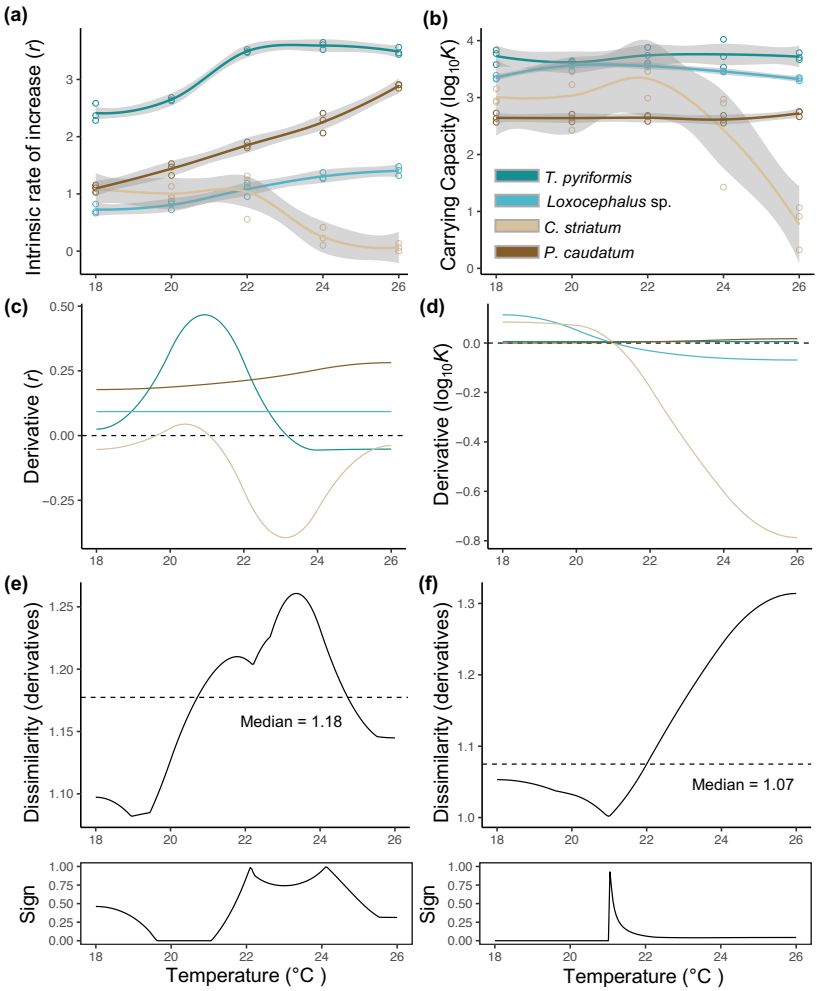
processes and functions, such traits are now termed *effect* traits, while *response* traits aim to capture information about how a species responds to environmental change (Suding *et al.* 2008; Oliver *et al.* 2015), though such information is not always well captured by putative functional traits (Bartomeus *et al.* 2017). Examples of response traits include life-form and seed mass in plants (Sasaki *et al.* 2019), aquatic stage and reproductive strategy in freshwater macroinvertebrates (Thornhill *et al.* 2018), and clutch size and thermal maximum in birds (Hordley *et al.* 2021). Response trait diversity is then typically measured as the functional dispersion (FDis) of the response trait space (Laliberté *et al.* 2010; Rader *et al.* 2013), or sometimes using the closely related Rao's Quadratic Entropy (RaoQ) index (Chillo *et al.* 2011; Correia *et al.* 2018). Some studies alternatively group species into functional response groups (*e.g.*, Joseph *et al.* 2014; Schweiger *et al.* 2015), where species within a functional group are posited to respond similarly to environmental change based on their response traits, but this approach ignores a suite of functional differences between species; functional grouping is rarely ecologically meaningful (Petchey & Gaston 2006).

Considerable challenges remain when quantifying functional diversity. For example, there is still no consensus on which traits are 'functional' in a range of systems (Violle *et al.* 2007), and many traits can be highly correlated with, for example, body size (Koziowski & Weiner 1997). When attempting to measure response trait diversity, it can be difficult to delineate responses from effects; many traits act both as response and effect traits (Hooper *et al.* 2005; Suding *et al.* 2008). Moreover, it is often practically challenging to measure functional traits in the field, particularly for mobile organisms (Pakeman & Quested 2007; Moretti *et al.* 2017). When measuring functional diversity from species traits, there is no single best metric for all scenarios, as most functional diversity indices capture different properties of the functional differences within a community (Villéger *et al.* 2008; Schleuter *et al.* 2010). Other methodological considerations include whether and how to abundance-weight functional diversity indices to account for rare species (Lavorel *et al.* 2008), and how to handle intraspecific trait variation given its ecological importance (de Bello *et al.* 2011; Albert *et al.* 2012; Ross *et al.* 2017). Together, these challenges hinder the empirical quantification of response diversity using functional response traits. As such, we suggest caution in measuring response trait diversity unless using well-defined and empirically tested response traits (*e.g.*, Kandlikar *et al.* 2022).

Box 2. Re-analysing response diversity for experimental aquatic communities

Here, we demonstrate the ease with which our statistical framework can be applied to empirical data, by reanalysing the variation in performance-environment relationships among aquatic microorganisms first presented by Leary and Petchey (2009). The original study assembled ciliate communities comprising four species (*Colpidium striatum*, *Loxocephallus* sp., *Paramecium caudatum*,

and *Tetrahymena pyriformis*) with measured responses to temperature across five levels (18, 20, 22, 24, and 26°C; Box Figure 1a,b). The authors then measured response diversity as the correlation between pairwise species responses to temperature, measured using two higher-level traits—intrinsic rate of increase (r) and carrying capacity ($\log_{10} K$)—and used this response diversity as a predictor of, among other things, community biomass (Leary & Petchey 2009). Here, we took a different approach to measure response diversity. We modelled each species' performance (r or $\log_{10}K$) individually using Generalized Additive Models (GAMs), and calculated the first derivates of each performance-temperature relationship (Box Fig. 1c,d); here producing *second* derivatives of abundance that indicate sensitivity to environmental change (Shyu & Caswell 2014). We then estimated the two dimensions of response diversity described above; we measured the dissimilarity of these first derivatives (Leinster & Cobbold 2012) and their sign-sensitivity (that is, the extent to which the first derivatives span zero for a given environmental context). In doing this as a function of temperature, we produced temperature-dependent estimates of response diversity, which was highest for r at around 23.5°C when performance-environment responses were divergent and zero-spanning (Box Fig. 1e), and highest for $\log_{10}K$ at the maximum temperature as the carrying capacity of *C. striatum* declines while the other species remain fairly constant (suggesting *C. striatum* has a disproportionate contribution to dissimilarity here). Note, however, that the sign-sensitivity of the derivatives is low at this temperature, so we might predict any community-level properties driven by carrying capacity to be unstable at high temperatures (Box Fig. 1f). Such temperature-dependent response diversity values provide an added layer of information—and hence predictive capacity—compared to the original analyses based on correlated performance-environment responses (Leary & Petchey 2009).



Box Figure 1. Re-analysis of data from Leary & Petchey (2009) using the framework proposed herein. Using empirical data from Leary & Petchey (2009), we measured performance-environment relationships for four aquatic ciliate species [coloured lines] as (**a**) the intrinsic rate of increase [*r*] and (**b**) the carrying capacity [$\log_{10}K$] along a temperature gradient (18-26°C). Data points are from a single population (see Figs. 1a and 2a in Leary & Petchey 2009). (**c**,**d**) We calculated the first derivatives of the performance-temperature relationships, which change as a function of temperature due to nonlinear responses. (**e**,**f**) We then measured the similarity-based diversity and sign-sensitivity of the derivatives of all species in the community for both (**e**) *r* and (**f**) $\log_{10}K$. (**e**) For *r* we found that both indices peaked around 22-24°C. (**f**) For $\log_{10}K$, dissimilarity peaked at the upper temperature limit, as the response of one species (*C. striatum*) diverged from the others (**b**,**d**), while the sign-sensitive index was mostly zero across the temperature range. Dashed lines indicate zero in panels **c** and **d**, and the median value of response diversity along the X-axis in panels **e** and **f**.

Acknowledgements

We thank Dan Leary for generating the empirical data we reanalysed in this study (Box 2). Thanks also to Jean-François Arnoldi and Ian Donohue for earlier discussion. This study was supported by a SHINKA collaboration grant awarded to SRP-JR by the Okinawa Institute of Science and Technology

Graduate University (OIST). SRP-JR and DWA were supported by subsidy funding to OIST. OLP was supported by the University of Zurich Research Priority Programme in Global Change and Biodiversity (URPP GCB) and by SNF project 310030_188431. TS was supported by a Fostering Joint International Research A (no. 19KK0393) from the Japanese Ministry of Education, Culture, Sports, Science and Technology.

Data availability statement

All data and R code necessary to reproduce the analyses and figures will be available in the Zenodo digital repository (and assigned a DOI) upon acceptance. For now, the GitHub repository can be accessed directly at:
https://github.com/opetchey/response_diversity_how_to_measure/releases/tag/v1.0-review

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