How to measure response diversity

Samuel R.P-J. Ross[1*], Owen L. Petchey[2], Takehiro Sasaki[3], David W. Armitage[1]

[1]Integrative Community Ecology Unit, Okinawa Institute of Science and Technology Graduate University, Onna-son, Okinawa, 904-0495 Japan.

[2]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zürich, Switzerland.

[3]Graduate School of Environment and Information Sciences, Yokohama National University, 79-7 Tokiwadai, Hodogaya, Yokohama, 240-8501 Japan.

Email: s.ross.res@outlook.com (SRP-JR); owen.petchey@ieu.uzh.ch (OLP); sasaki-takehiro-kw@ynu.ac.jp (TS); david.armitage@oist.jp (DWA).

ORCID: 0000-0001-9402-9119 (SRP-JR); 0000-0002-7724-1633 (OLP); 0000-0001-8727-9152 (TS); 0000-0002-5677-0501 (DWA).

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 relationship; functional diversity; resilience; functional trait; temporal variability; functional response; insurance hypothesis; nonlinear dynamics.

Article type: Review

Words: Abstract 232 words; main text 7,863 words; box 488 words.

Display items: 5 figures; 0 tables; 1 text box.

***Correspondence**: Samuel R.P-J. Ross, Integrative Community Ecology Unit, Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna-son, Kunigami-gun, Okinawa, 904-0495 Japan. E: s.ross.res@outlook.com

Abstract

1. The insurance effect of biodiversity—that diversity enhances and stabilises aggregate ecosystem properties—is mechanistically underlain by inter- and intraspecific trait variation in organismal responses to environmental change. 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.
2. Here, we review methods for measuring response diversity and from them distil a methodological framework for quantifying response diversity from experimental and/or observational data, which can be practically applied in lab and field settings across a range of taxa.
3. Previous empirical studies on response diversity most commonly invoke functional response traits as proxies aimed at capturing functional responses to the environment. 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. Given its derivation from empirical data on functional responses, this approach should more directly reflect response diversity than the trait-based approach dominant in the literature.
4. 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 conserving this critical dimension of biodiversity.

1. Introduction

Ecological stability has been a core focus of ecology since the 1950s when interest in the relationship between diversity and stability arose (McCann 2000). Ecological stability is a multidimensional concept encompassing a variety 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 (that is, 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 theoretical developments (*e.g.*, McCann *et al.* 1998; Kondoh 2003; Ives & Carpenter 2007) have reached the consensus that in more complex models which include, for example, variable environments, interaction strengths, or behaviours, species-rich systems will exhibit less stable (that is, more variable) aggregate 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 some emergent ecosystem-scale function (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), which posits 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 tractable 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.* 2022a); and asynchronous or compensatory dynamics (Gonzalez & Loreau 2009; Wang *et al.* 2021) among species 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). For example, 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; see also Houlahan *et al*. 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 frequently 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 result from 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 intrinsic 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 a key candidate underlying several of these interrelated potentially key processes: response diversity.

2. Existing response diversity studies

Few empirical studies have explicitly measured response diversity. Recognising 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 (Figure 1). These empirical

studies used various methods to measure response diversity. The majority (*n* = 28 studies, ~60%) used 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) following Elmqvist *et al.* (2003), 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; Figure 1). This binary approach asks, "is there response diversity among species or not?" 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 estimate 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 pairwise 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 (Figure 1) have emerged independently, resulting in a disconnect among empirical response diversity studies, and a general methodological framework for measuring response diversity is lacking.

In response to this, in the remainder of this article we present a framework for measuring response diversity empirically using performance-environment relationships (Section 3), including application to simulated data for linear (Section 3.1) and nonlinear functional responses (Section 3.2), where the form of the performance-environment relationship depends on environmental context, as well as an application to an empirical dataset of multispecies aquatic microcosms (Section 3.3). Finally, we discuss future directions for empirical studies of response diversity and the challenges of applying this approach in a range of contexts (Section 4).

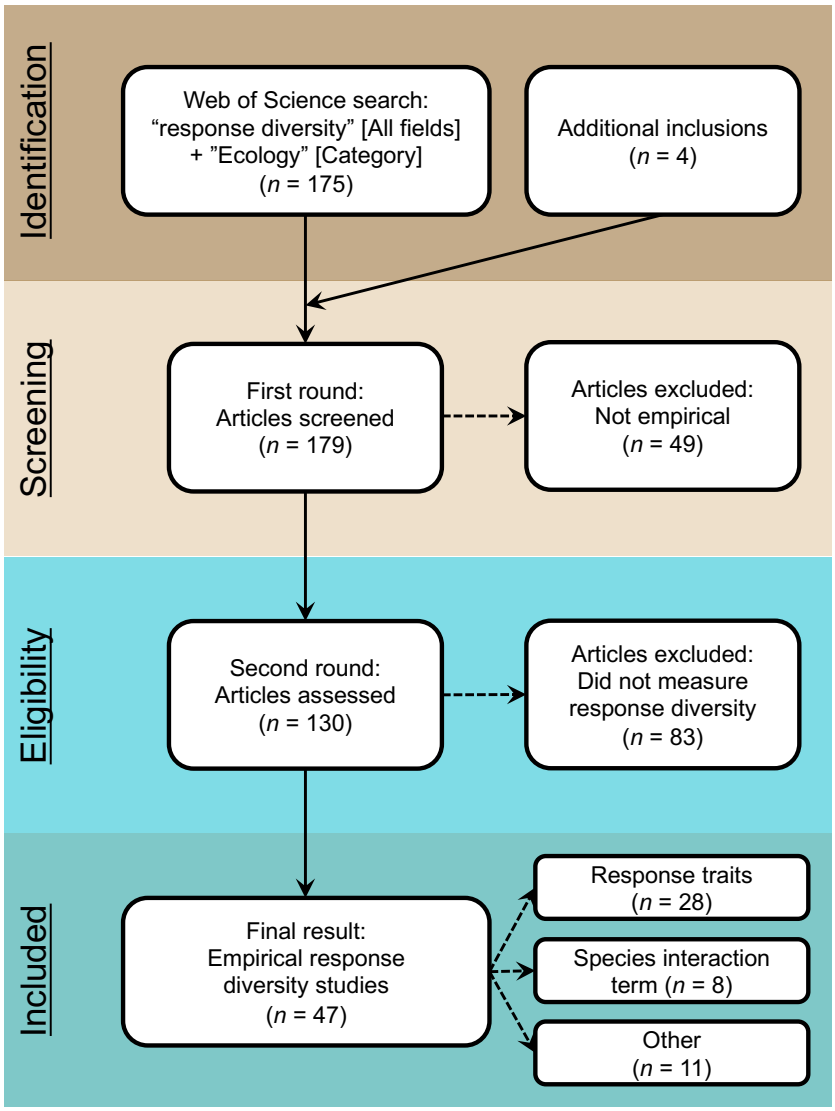

Figure 1. PRISMA diagram detailing the results of our systematic review. On 17 Dec 2021, we conducted a Web of Science search for "response diversity" in all fields within the "Ecology" Web of Science category. We supplemented the resulting 175 papers with four that we knew to be relevant but were not 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.).

3. 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. That said, low-level traits can still be used in this framework, and can in some cases be informative and important responses (*e.g.*, stand-level Nitrogen content).

Our aim is not to define a single best metric of response diversity for use in all cases, but rather to illustrate how it can be measured. We demonstrate two complimentary metrics with desirable properties for our purposes. More suitable metrics for different use-cases likely exist, and we encourage researchers to explore various methods while warning against the proliferation of untested response diversity metrics—a new metric should necessarily be an improvement on existing metrics in its ability to fulfil its purpose (see Figure 5 below). In response diversity's case, this purpose is to predict ecological stability, as grounded in the basic principles of the insurance hypothesis (Yachi & Loreau 1999).

We propose extending 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 estimate of how species respond to the environment than, for example, the often-used functional response trait approach (Box 1), and allows identification of key contributors to response diversity (Leary & Petchey 2009). Given our definition of *performance*, the response variable in such models 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 a species contributes (Figure 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; Figure 2b), or in response to the abundance of a predator, competitor, or the availability of a prey species (*e.g.*, Fauchald *et al.* 2011; Figure 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). Similarly, modelling biomass change in response to a competitor is akin to concepts in coexistence theory such as negative density-dependence (*e.g.*, Armitage & Jones 2019) or invasion growth rate (Grainger *et al.* 2019).

3.1. Measuring variation among performance curves

From such models, we suggest measuring response diversity as the variation in the slope (first derivative) 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 (Figures 2a-2c), then taking the first derivatives of these models to estimate model slopes along the environmental axis (Figures 2d-2f), though note it may not always be necessary to calculate the derivatives of a performance variable that is already a rate measure, in which case the fitted GAM function would suffice. 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 Ross *et al.* 2022b). Response diversity can then be measured as the variation in the distribution of these derivatives to capture the variation in species-specific environmental responses (Figures 2g-2i). In practice, this variation could be described using any suitable estimator, but here we use two complementary metrics.

First, we use a similarity-scaled metric 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 the (dis)similarity metric can use information on species relative abundances within an 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 (for details see

Leinster & Cobbold 2012; Ross *et al.* 2022b). 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 (Figure 2g), and highest (*S*) when species responses are as dissimilar as possible (the estimator converges to species richness as performance-environment slopes diverge to infinity and –infinity).

Second, we develop a measure that accounts for whether performance-environment responses *diverge* in direction, since this should be a key indicator of the stabilising potential of response diversity under a given environmental condition. The insurance effect of biodiversity assumes that declines of one species can be offset by neutral or positive responses of others (Yachi & Loreau 1999). As such, we also isolate and measure this property of response diversity using the formula:

$$\text{Divergence} = \frac{(\max[f'(E)]-\min[f'(E)])-\left||\max[f'(E)]|-|\min[f'(E)]|\right|}{(\max[f'(E)]-\min[f'(E)])},$$

where $f'(E)$ represents the first derivative of a performance-environment relationship, $f(E)$, at a particular environmental state *(E).* If the range of derivatives does not span zero (*e.g.*, Figures 2d and 2e), 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 divergence axis of species responses (the value is zero). Without interspecific interactions, even large differences in the magnitude of response (that is, the metric of response diversity discussed above) cannot be stabilising (Ives *et al.* 1999; Mougi & Kondoh 2012). In contrast, when derivatives are perfectly symmetric around zero, the value is one. When the range of first derivatives spans zero for a given environmental state (*e.g.*, Figure 2f), species responses are diverging (at least one species is decreasing while another is increasing), which we expect *a priori* to be stabilising. This divergence metric is largest (1) when $\min[f'(E)] = -\max[f'(E)]$. Observation of stable aggregate ecosystem properties (*e.g.*, biomass) when the range of performance-environment derivatives does *not* span zero, would suggest that response diversity is not the mechanism driving stability in that case.

Together, the similarity-based diversity metric and divergence metric make up two complimentary components of response diversity. The specific metrics we use here may not be ideal for all use cases. Further work should thus consider the need to develop suitable metrics 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 metrics for quantifying response diversity in a range of contexts (Figures 2 and 3), including applications to real data (Figures 4 and 5).

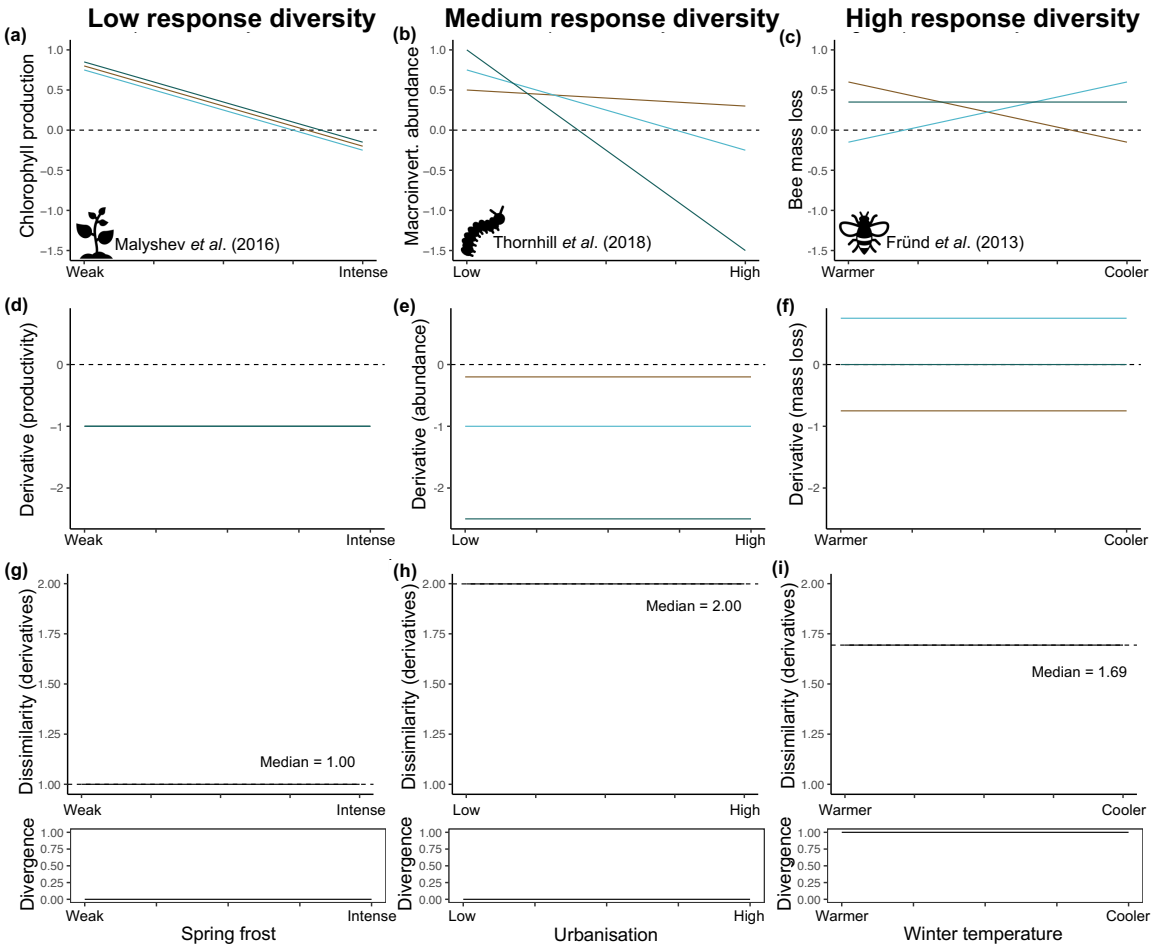

Figure 2. Measuring response diversity for linear species-environment relationships. We reimagined the original analyses of three studies, using standardised, simulated data to demonstrate how response diversity could be measured practically under our framework. (**a**) We propose a hypothetical case (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 the proposed similarity-based diversity metric (see main text), and find it to be one (its lower bound), since all species respond identically to spring frost. Our divergence metric 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 divergence 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, divergence 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 metric (dissimilarity) along the X-axis in panels **g**–**l** (here, equivalent to any value along the X-axis since response diversity is constant).

3.2. Nonlinear responses to environmental variation

Ecological responses to the environment are often nonlinear, necessitating a wide range of statistical tools for considering such responses. 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 derivatives) is robust to nonlinearities such as species' functional responses to competition, predation, or resource availability (Figure 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 (Figure 3a); one where seedling establishment responds to grazing pressure with higher response diversity among species (Figure 3b); and one where trees respond nonlinearly to fire frequency, and diverge in their responses (Figure 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; Figures 3f and 3i). Where responses are nonlinear, the derivatives of performance-environment responses vary as a function of the environmental variable (along the X-axis in Figures 3d-3f). In turn, this produces an estimate of response diversity that also varies as a function of the environment (Figure 3g-3i). Using these hypothetical examples, we see that the performance variables of interest should be stable only over a narrow range of environmental conditions in the case of flowering plant abundance (Figure 3g), whereas seedling establishment and tree density are predicted to be stable over a wider set of environmental conditions (Figures 3h and 3i). 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-3i), though it may be appropriate to weight such a summary statistic by the distribution of the environmental variable. In linear cases (Figure 2), response diversity does not vary with environmental context, so summary statistics are not needed.

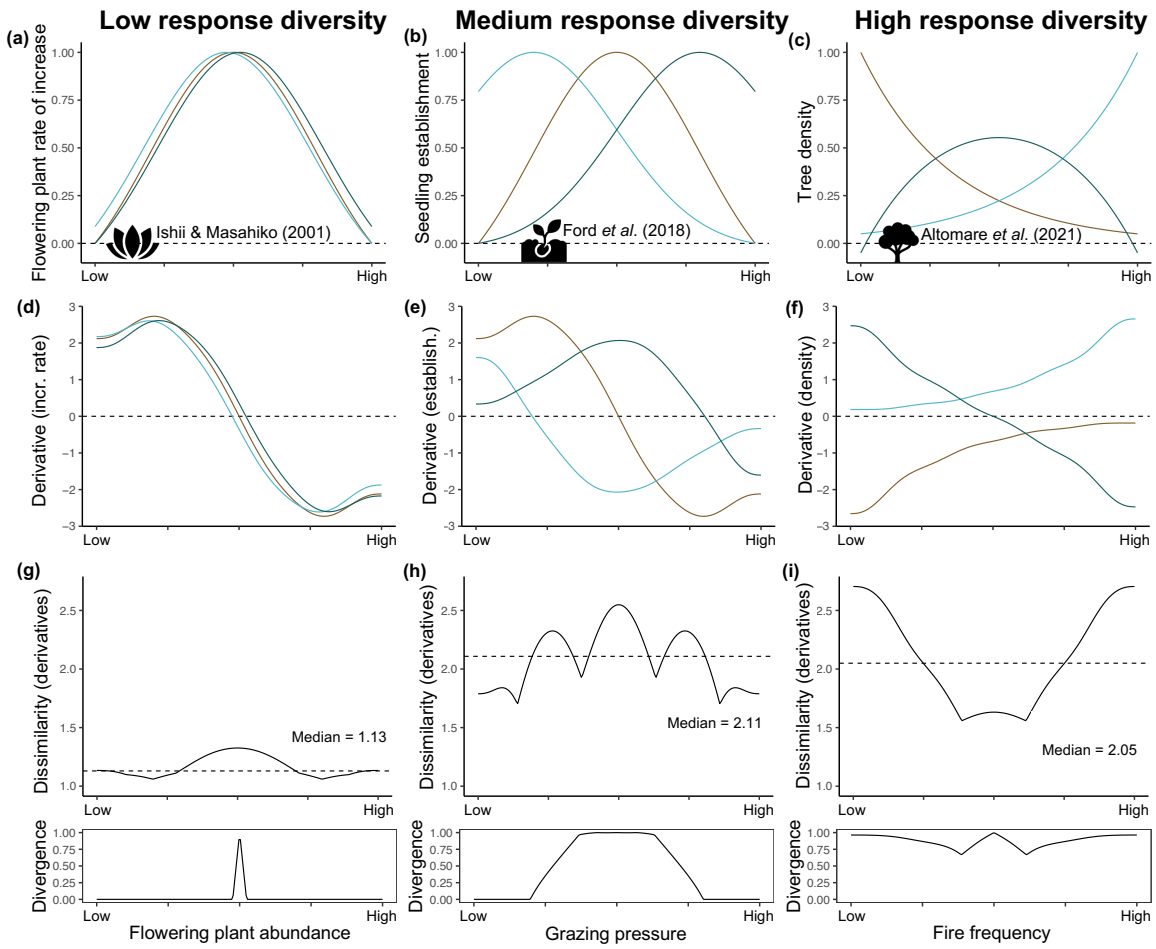

Figure 3. Measuring response diversity for nonlinear species-environment relationships. We reimagined the original analyses of three studies, using standardised, simulated data to demonstrate how response diversity could be measured practically under our framework. (**a**) We propose a hypothetical case (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 divergence—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 binary 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 (dissimilarity and divergence) that should drive ecological stability as described under the insurance hypothesis (Yachi & Loreau 1999), 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.*, Figure 2b), thus producing *rates* from which we calculate response diversity (Figure 2e). However, it is also possible to estimate derivatives of rates (*e.g.*, Figures 3d and 4), 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 researchers 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; Ross *et al.* 2022b).

Using the framework for measuring response diversity we present here, one can measure response diversity empirically in the laboratory or field. A conceptually simple and empirically tractable metric of response diversity can stimulate research on a range of previously unanswerable 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). In turn, this 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.

3.3. Revisiting the response diversity-stability relationship in experimental aquatic communities

Next, as an empirical proof-of-concept for our framework, we demonstrate how it can be used to measure response diversity among aquatic microorganisms first presented by Leary and Petchey (2009). The original study involved four ciliate species (*Colpidium striatum*, *Loxocephallus* sp., *Paramecium caudatum*, and *Tetrahymena pyriformis*). The first empirical step was to measure the responses of each species alone to temperature (five levels: 18, 20, 22, 24, and 26°C; Figures 4a and 4b). Responses of two types of performance were measured: intrinsic rate of increase (r) and carrying capacity ($\log_{10} K$). These two properties (r and $\log_{10}K$) provide complementary information on species' performance, each with relevance at different temporal scales. For example, r is likely of more relevance if the environmental change of interest occurs rapidly or is short-lived, since r provides information on a population's ability to rapidly bounce back after disturbance. Conversely, $\log_{10}K$ may be most relevant over longer temporal scales of environmental change, since populations are unlikely to reach carrying capacity immediately following disturbance. The second empirical step was to record the biomass dynamics of communities that contained different combinations of the four species, and which were exposed to different ranges of temporal variation in temperature. The analyses involved calculating the response diversity present in each of the communities, and comparing this to the stability of the biomass dynamics of the communities (Leary & Petchey 2009).

Here, we took a different approach to measure response diversity than in the original study. 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 (Figures 4c and 4d). We then estimated the two dimensions of response diversity described above; we measured the dissimilarity of these first derivatives (Leinster & Cobbold 2012) and their divergence (the extent to which derivatives span zero for a given temperature). In doing this as a function of temperature, we produced temperature-dependent estimates of response diversity, which were highest for r at around 23.5°C when performance-environment responses were divergent and zero-spanning (Figure 4e), 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 divergence 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 (Figure 4f). 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).

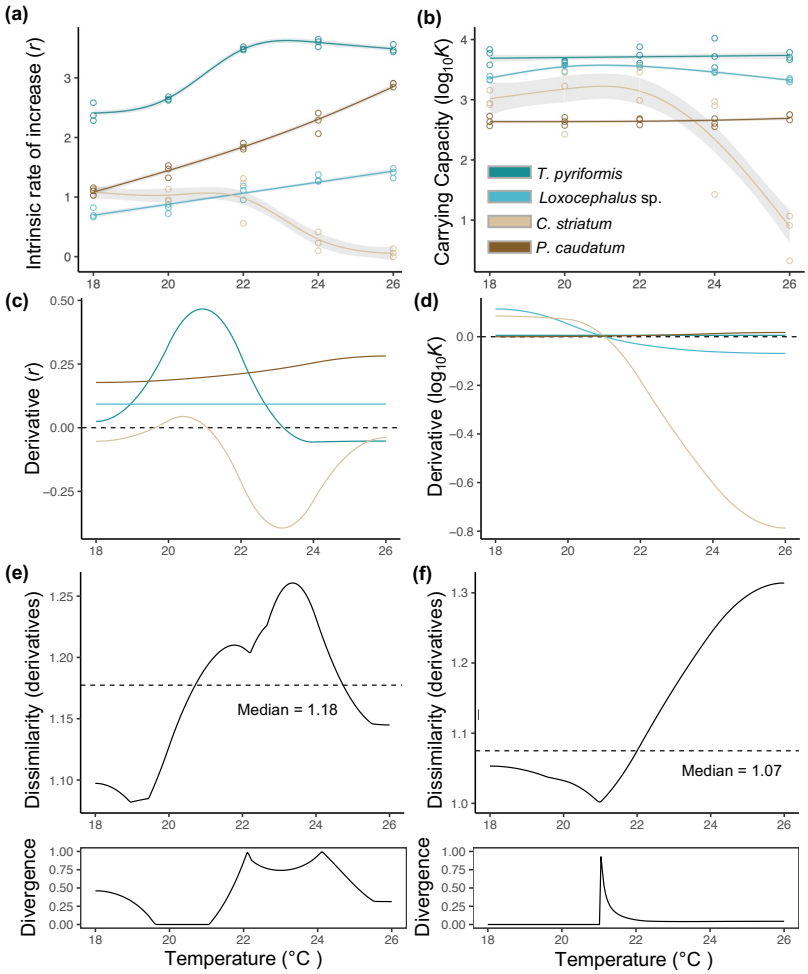

Figure 4. Re-analysis of data from Leary & Petchey (2009) using the framework proposed herein. Using empirical data from Leary & Petchey (2009), we measured performance-environment relationships for four aquatic ciliate species [coloured lines] as (**a**) the intrinsic rate of increase [*r*] and (**b**) the carrying capacity [$\log_{10}K$] along a temperature gradient (18-26°C). Data points are from a single population (see Figures 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 divergence 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 divergence 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**.

Just as metrics measuring functional diversity with effect traits should be related to ecosystem functioning (Cadotte *et al*. 2011), response diversity measures should explain and/or predict community stability. Next, we assess this explanatory power, again using Leary and Petchey's (2009) aquatic ciliate experiment. To do so, we compared the relationship between response diversity and community stability of pairs of ciliate species. Stability is defined here as the coefficient of variation (ratio of the standard deviation to the mean) of pairwise total ciliate biomass (Donohue *et al.* 2013).

We calculated six measures of response diversity—three types of measure applied separately to the r and $\log_{10}K$ response curves. We calculated the two metrics of response diversity discussed above: the Leinster and Cobbold (2012) similarity-based measure, and the divergence measure aimed at capturing whether species responses differ in their direction. We also calculated a measure similar to that in the original study: the correlation of the responses of the species in each community.

When modelling the relationship between each response diversity metric and community stability using a simple linear regression (Ross *et al*. 2022b), we were able to assess the performance of different measures of response diversity. We found that for the intrinsic rate of increase, our proposed divergence metric outperformed other metrics of response diversity, including that from the original study (Figure 5a). Across our examples for both r and $\log_{10}K$, the relationship between divergence and community stability of r was the only significant relationship (the only model slope with confidence intervals not spanning zero; Figure 5). This metric thus represents an advance when aiming to predict community stability of r, though the Leinster and Cobbold (2012) method was not a significant improvement, and divergence did not improve the relationship with $\log_{10}K$ stability (we found similar results when measuring covariance-based stability; Ross *et al*. 2022b). Future efforts should thus use this example as a springboard from which to explore a wider range of response diversity methods, using data from various case studies, with the explicit goal of benchmarking any proposed new response diversity metric against existing approaches to determine which method best predicts community stability. In doing so, methods development should not deviate from response diversity's *a priori* theoretical aim to reflect the diversity of species responses to the environment and, in turn, to mechanistically drive ecological stability (Yachi & Loreau 1999).

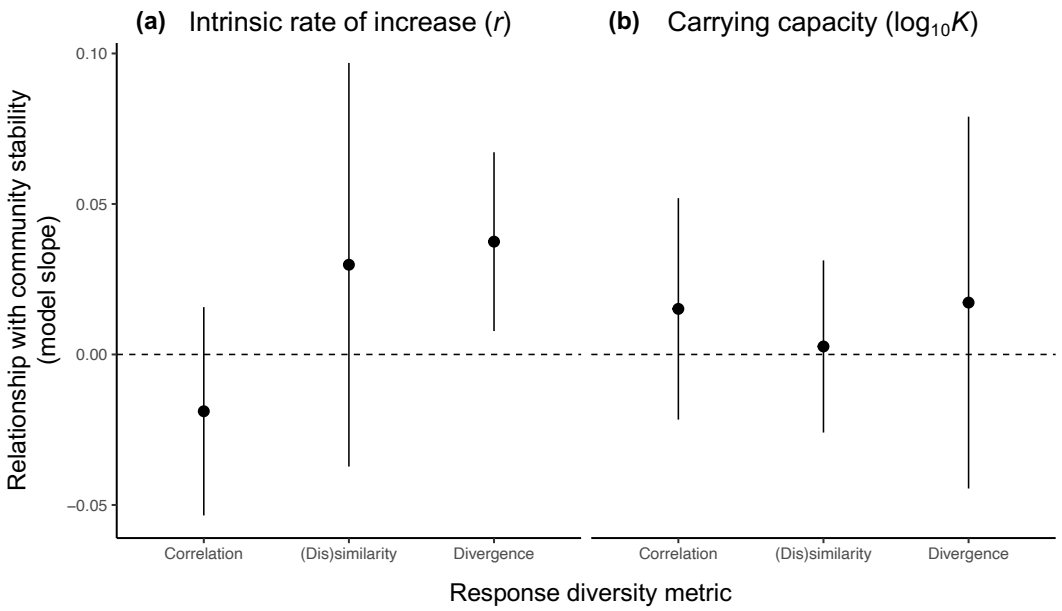

Figure 5. Comparison of predictive power of response diversity metrics for data from Leary & Petchey (2009). After measuring response diversity for Leary & Petchey's (2009) ciliate dataset using the framework proposed herein, we compared the ability of response diversity to predict community stability (the coefficient of variation of total biomass for each pairwise combination of ciliate species; see Leary & Petchey 2009; Ross *et al.* 2022b). Predictive power is approximated by the model slope (± 95% confidence interval) of the response diversity-stability relationship; where confidence intervals do not span zero above or below zero, this indicates a significant positive or negative relationship, respectively. We tested three measures of response diversity: 1) a pairwise correlation-based measure from the original Leary & Petchey (2009) study (*Correlation* on x-axis); 2) the Leinster & Cobbold (2012) similarity-based measure described therein (*(Dis)similarity*; Ross *et al.* 2022b); and 3) the divergence metric measuring the proportion of zero-spanning species' derivatives (*Divergence*). Left panel (**a**) represents response diversity and community stability measured from the Intrinsic rate of increase, while (**b**) is measured from the $\log_{10}$ carrying capacity (Leary & Petchey 2009; Ross *et al.* 2022b). See Ross *et al.* 2022b for figures showing individual response diversity-stability relationships and a complementary model slope figure relating response diversity to stability calculated using covariance rather than coefficient of variation.

4. Future directions and challenges

The framework for measuring response diversity introduced above is conceptually simple and applicable across contexts. Using this approach, response diversity can be easily measured in empirical settings (see Figure 4 for reanalysis of data from Leary & Petchey 2009), experimentally manipulated, and related to stability (Figure 5), offering advantages over the less direct estimates of species responses provided by the functional trait approach dominant in the literature (Box 1)—though future work should make direct comparisons between response diversity measured using performance-environment relationships and those estimated using functional response traits.

4.1. Interspecific interactions

The performance-environment relationships we mention above can be established in isolation and then community level response diversity calculated from individual species responses. However, this approach neglects any interspecific interactions within multispecies communities. Indeed, the current concept of response diversity assumes that species-species relationships are less important for stability than abiotic environmental effects on species (that is, species-environment relationships; Ives & Carpenter 2007). Yet this assumption is not a limitation for two main reasons. First, one could simply model species responses (individually, using species-specific GAMs; Ross *et al.* 2022b) 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). Second, theoretical and empirical studies show that species-environment relationships are often more important that species-species relationships in driving stability (*e.g.*, Houlahan *et al*. 2007; Ives & Carpenter 2007). That interspecific interactions need not be included when measuring response diversity is thus not necessarily a limiting assumption, but rather a realistic one. That said, future work should establish the relevance of different interaction types when measuring response diversity empirically.

4.2. Multifarious environmental change

The framework above focuses on derivation of environment-dependent performance responses when a single environmental variable is varying. Yet, species and communities are often perturbed by multiple environmental stressors simultaneously. Rather than using response diversity solely as a predictor variable for estimating univariate stability responses, a system's response along an environmental gradient could be measured as a function of a second environmental condition. That is, response diversity can be assessed for a given environmental state and compared to other treatments or replicates across any environmental ranges of interest, permitting quantification of response diversity to multiple environmental stressors, which often occur simultaneously (Dieleman *et al*. 2012; Bowler *et al.* 2020). Another approach, which we aim to develop, would be based on multivariate response surfaces (*e.g.*, Yang *et al.* 2022). With this, multivariate response diversity may link conceptually to the study of co-tolerance to multiple stressors and stress-induced community sensitivity (see Vinebrooke *et al.* 2004) and should prove more operationalizable than univariate approaches given the propensity for multiple environmental stressors to not only co-occur but to interact nonadditively in nature (Dieleman *et al*. 2012).

4.3. Abundance and scale-dependence

Response diversity depends on the identities and likely also relative abundances of species within the community or functional group of interest. Thus, if community composition changes as a function of the environment, then response diversity should either be abundance-weighted to account for species losses and gains along the environmental gradient—for example, by changing the parameter q involved in the calculation of the similarity-based metric used herein (Leinster & Cobbold 2012). Species identities and abundances vary as a function of scale, making response diversity scale dependent. Practical users of response diversity should be careful not to extrapolate results beyond the focal temporal or spatial scale, given that ecological stability and its drivers vary in time and space (Ross *et al*. 2021b; Jarillo *et al*. 2022). Disturbance also has a temporal and spatial signature, meaning that the spatiotemporal scale of reference determines the environmental conditions and potential disturbances to which ecological communities are subject (Zelnik *et al*. 2018). Thus, response diversity measured over short timescales does not represent a holistic picture of how communities are likely to respond to the environment (that is, response diversity's goal to mechanistically capture the insurance capacity of a system), since the range of environmental conditions experienced at shorter scales may be limited when compared to longer temporal windows (Zelnik *et al*. 2018; Ross *et al*. 2021b). Despite the context-dependencies outlined here, response diversity has the potential to be a powerful tool for predicting ecological stability. Future studies should determine the temporal or spatial scales over which metrics of response diversity perform best when aiming to predict ecological stability and whether the methods presented here require further refinement to better reflect the insurance capacity of ecological communities across scales.

4.4. Individual species contributions

Another extension of this framework would consider the relative importance of each species to community-level response diversity by, for example, measuring the median dissimilarity in performance-environment model slopes between each species and all others in the community. In this case, the species with the greatest dissimilarity from the others should be the largest contributor to response diversity (*e.g.*, *Colpidium striatum* in Figure 4d), and thus be the species whose loss from the community should most greatly reduce response diversity and erode stability (provided the two are mechanistically linked). Such an approach complements studies considering the contribution of individual species to ecological responses and stability (*e.g.*, Donohue *et al.* 2017; White *et al.* 2020; Ross *et al.* 2021a, 2022a), in turn, aiding progress towards targeted conservation management decisions based on the quantifiable importance of individual taxa. Likewise, relative abundance and evenness may be important when considering the contribution of species to response diversity and

stability. The similarity-based diversity metric we used here is based on hill numbers, with an initial value of $q = 0$ indicating a focus on species richness. By increasing q to 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 in shaping response diversity (*e.g.*, Sasaki & Lauenroth 2011). Importantly, the subjects of response diversity analyses 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).

4.5. Data resolution and spatiotemporal scale

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. The same is true if measuring response diversity from observational time series; though response diversity may be a key biotic mechanism underlying the insurance effect of biodiversity (Yachi & Loreau 1999), observational time series do not afford us information on causal relationships (but see *e.g.*, Ushio *et al*. 2018). For response diversity to be measurable from observational data, time series should comprise higher-level traits as described above (*e.g.*, measuring intrinsic—that is, unlimited by competition—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 nonlinear responses, and response diversity experiments should be designed with sampling resolution in mind to sufficiently capture all possible forms of performance-environment relationships. Compared to controlled experiments, observational data from the field is often 'noisy', requiring additional care when measuring response diversity. As well as ensuring appropriate performance variables (*e.g.*, vital rates) are measured that capture some aspect of species' fitness or ecosystem functioning, one should aim to account for as many potentially confounding variables as possible when relating response diversity to stability, and to bear in mind that field studies rarely include all species from the regional pool, meaning response diversity is unlikely to portray the insurance capacity of the whole community. Future work should demonstrate the potential application of our response diversity framework to noisy field data. While the methods we describe here are useful for measuring stability from experimental or observational time series, response diversity could 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 at a given spatial scale (Loreau *et al.* 2003; Lamy *et al.* 2019; Wang *et al.* 2019, 2021).

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 measure response diversity at multiple sites across geographical regions, or to project locally-measured response diversity to other locations. Though our response diversity framework produces results that are necessarily a function of the environmental conditions against which species' performances are assessed, comparing response diversity to relevant local environmental stressors across sites is informative insofar as it should predict stability. A global-scale analysis of response diversity to locally relevant environmental conditions should therefore unveil macroecological patterns and hotspots of ecological stability (Capdevila *et al.* 2022), which in turn, should prove useful when making resilience-based conservation management decisions (Allen *et al*. 2011).

4.6. Environment-dependent response diversity for predicting stability-environment relationships

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 the environment are common, and include functional responses to prey availability (Holling 1966; Daugaard *et al.* 2019), and physiological responses to light and temperature (*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, these can lead to environmentally dependent 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 permits identification of the specific environmental conditions under which response diversity should or should not be stabilising. For a nonlinear environmental response, $f(E)$, one can examine the values of E (the 'environment') for which the derivatives of performance-environment relationships, $f'(E)$, including their confidence regions, diverge (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. This should complement existing studies of the impact of environmental

conditions on ecological stability (*e.g.*, Hillebrand *et al.* 2018; Ross *et al.* 2022a) by identifying possible underlying biotic drivers of environmental responses. Moreover, in cases where response diversity varies as a function of the environment (that is, where performance-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 relates to stability. There is still much 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.

5. Conclusion

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 empirical studies of response diversity were rare, and where they did occur, most measured 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 (Bartomeus *et al.* 2017; Box 1), we suggest measuring response diversity more directly, as the variation in performance responses to environmental conditions (Leary & Petchey 2009; Thibaut *et al.* 2012). The framework we propose herein provides a direct, empirically tractable, and conceptually simple estimate 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.

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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. However, 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, such as specific leaf area or photosynthetic pathway (Sasaki *et al*. 2019), 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 aspects 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).

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Acknowledgements

We thank Dan Leary for generating the empirical data we reanalysed in this study, and Jean-François Arnoldi, Helmut Hillebrand, Charlotte Kunze, and Frank Pennekamp for helpful 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 are available in the Zenodo digital repository https://doi.org/10.5281/zenodo.7018707 (Ross *et al*. 2022b).

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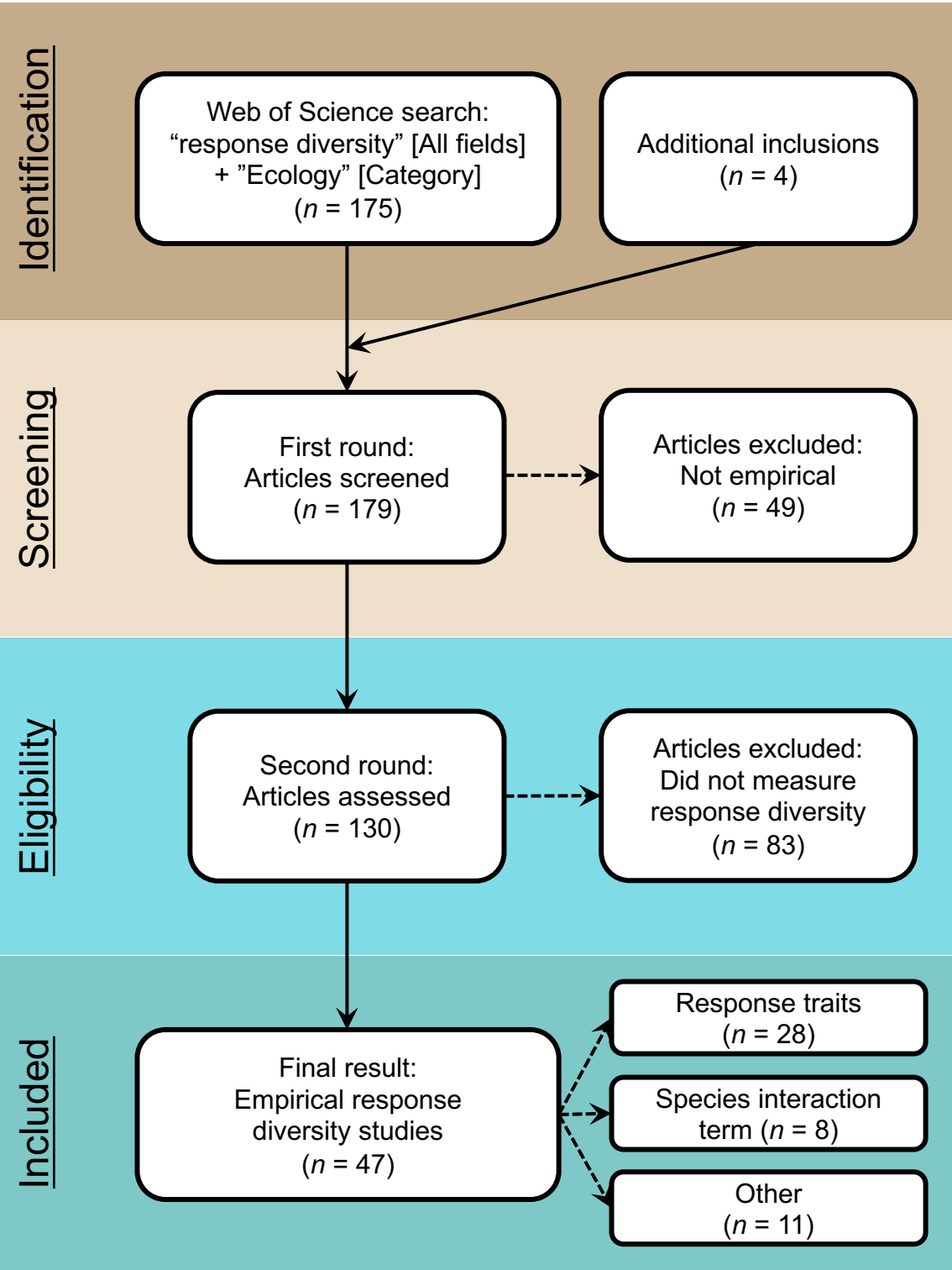
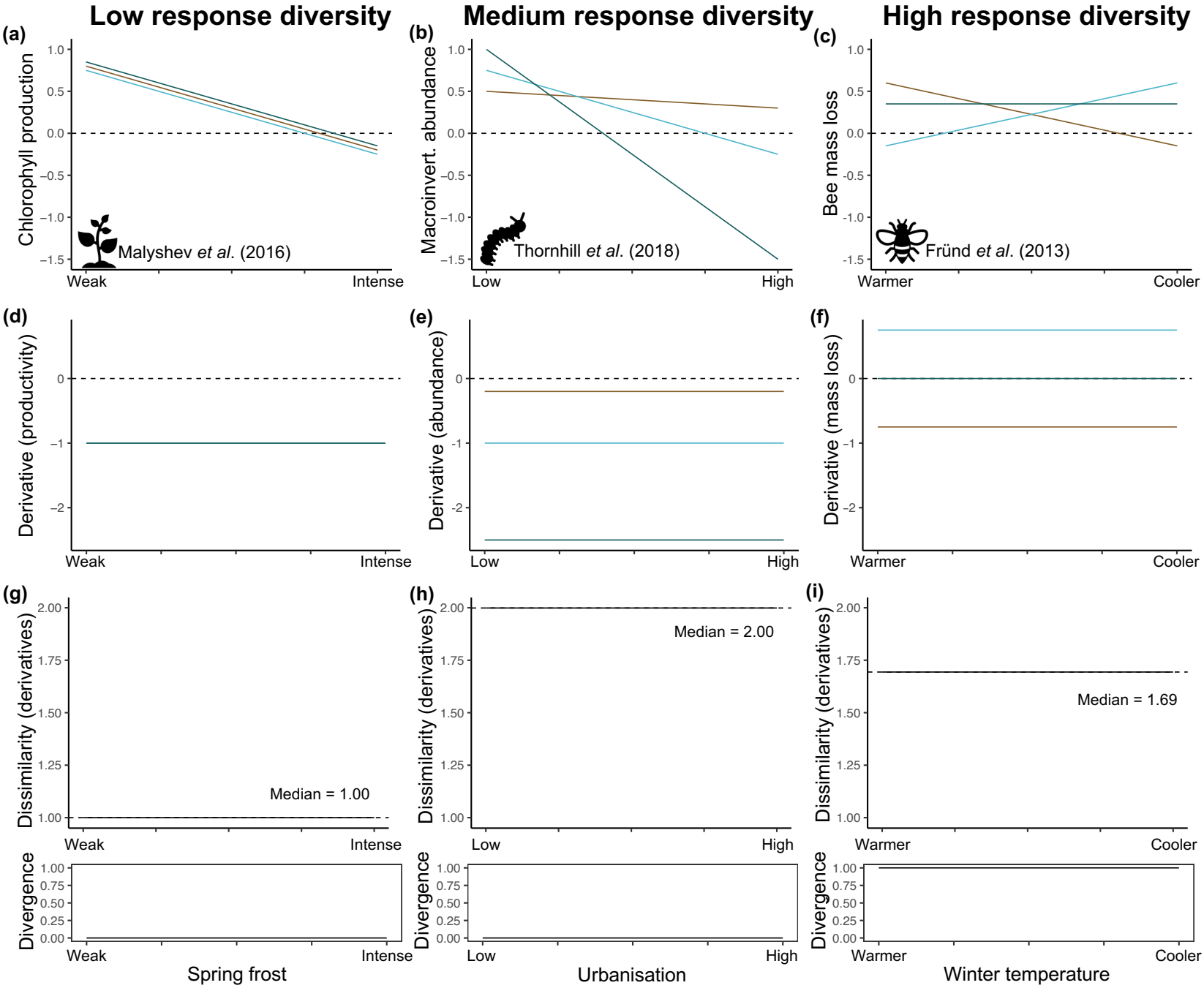
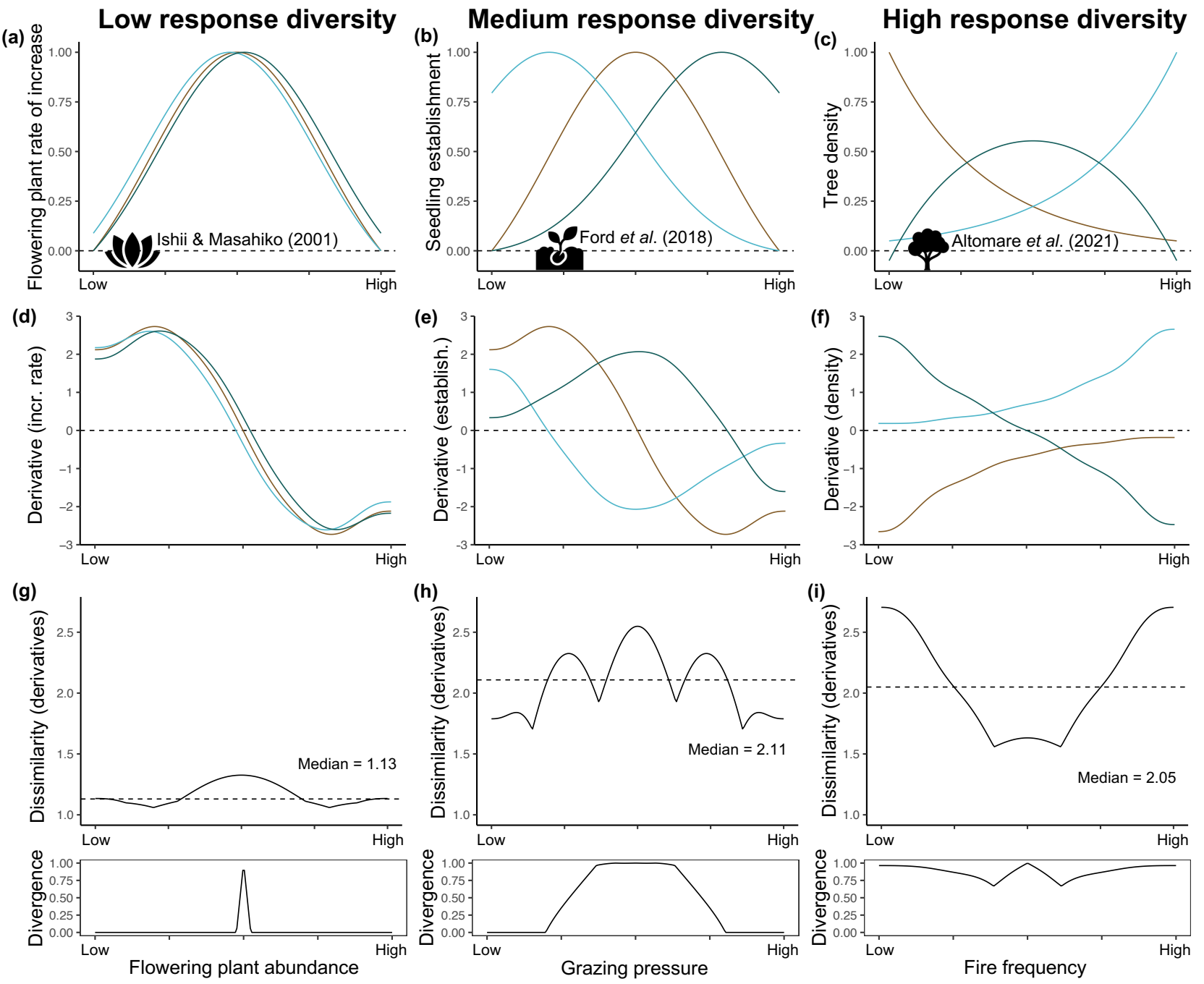
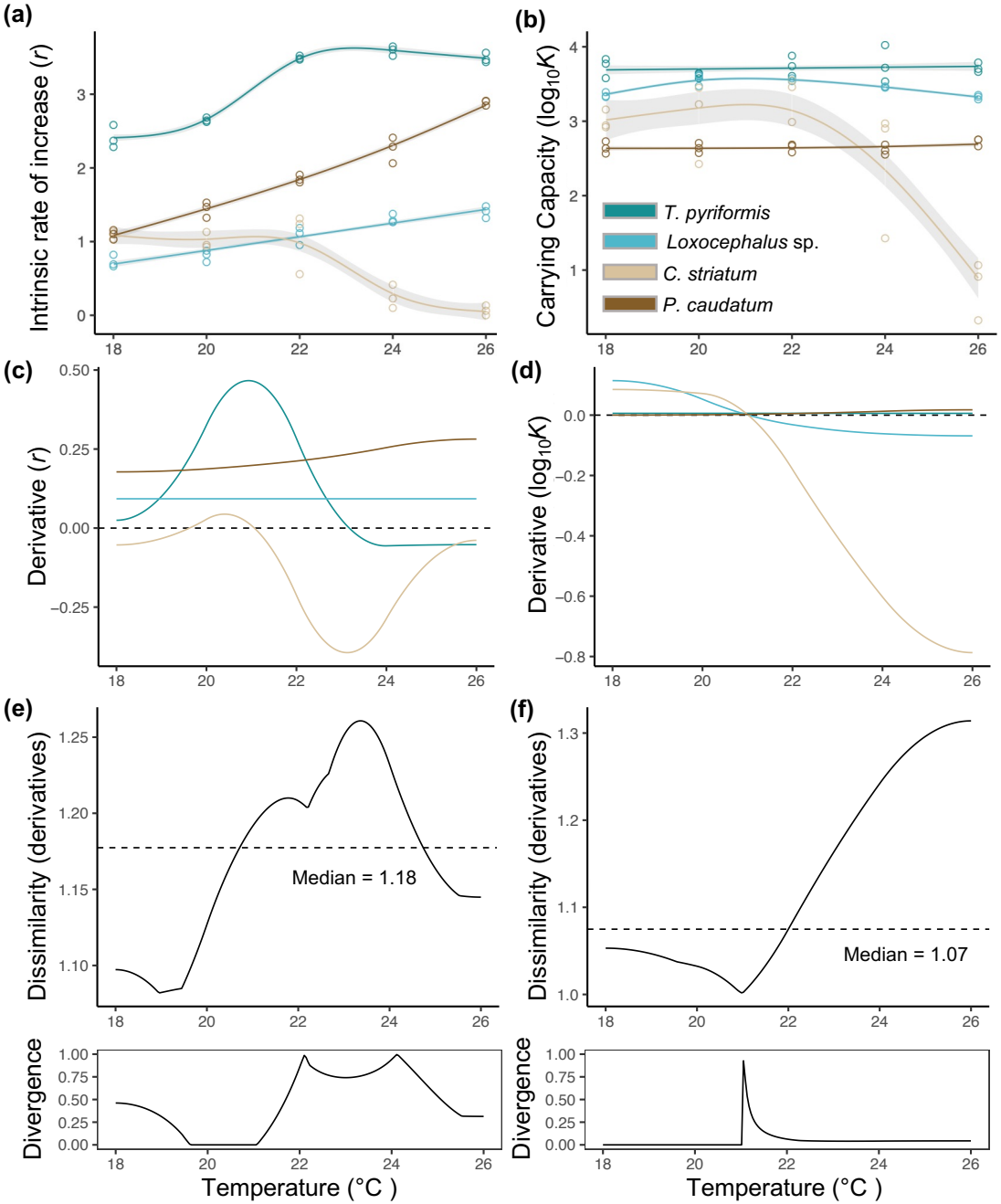
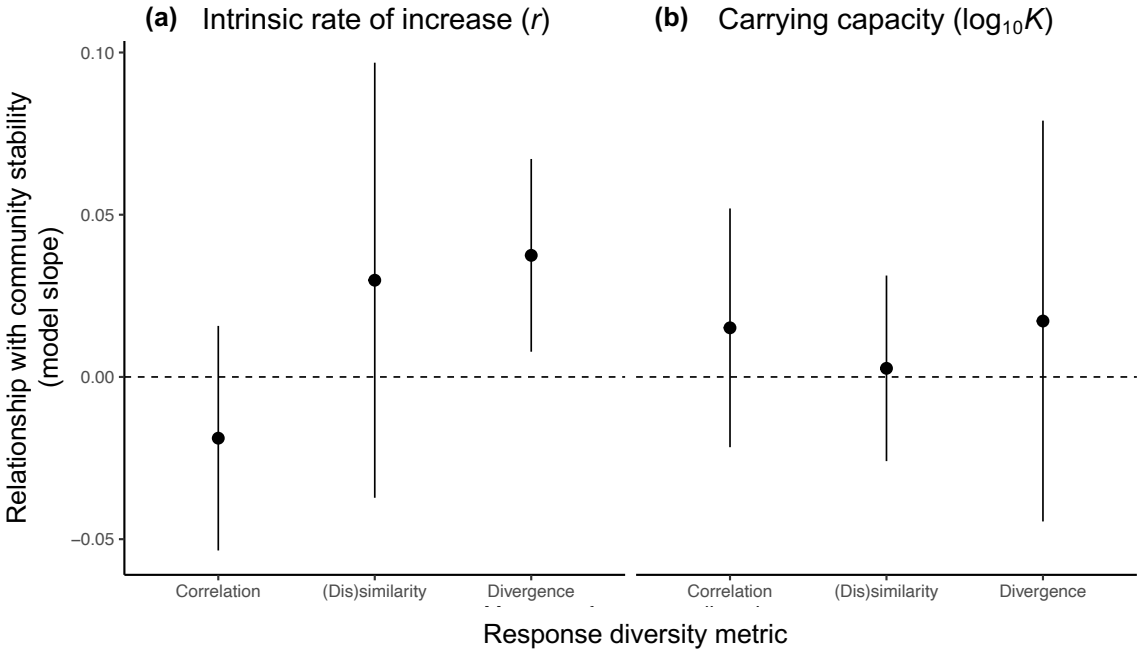

Identification
Web of Science search:
“response diversity” [All fields]
+ ”Ecology” [Category]
(n = 175)
Additional inclusions
(n = 4)
Screening
First round:
Articles screened
(n = 179)
Articles excluded:
Not empirical
(n = 49)
Eligibility
Second round:
Articles assessed
(n = 130)
Articles excluded:
Did not measure
response diversity
(n = 83)
Included
Final result:
Empirical response
diversity studies
(n = 47)
Response traits
(n = 28)
Species interaction
term (n = 8)
Other
(n = 11)


Low response diversity
Medium response diversity
High response diversity
(a)
(b)
(c)
Chlorophyll production
Macroinvert. abundance
Bee mass loss
Malyshev et al. (2016)
Thornhill et al. (2018)
Fründ et al. (2013)
Weak
Intense
Low
High
Warmer
Cooler
(d)
(e)
(f)
Derivative (productivity)
Derivative (abundance)
Derivative (mass loss)
(g)
(h)
(i)
Dissimilarity (derivatives)
Median = 1.00
Median = 2.00
Median = 1.69
Divergence
Spring frost
Urbanisation
Winter temperature


Low response diversity
Medium response diversity
High response diversity
(a)
(b)
(c)
Flowering plant rate of increase
Seedling establishment
Tree density
Ishii & Masahiko (2001)
Ford et al. (2018)
Altomare et al. (2021)
Low
High
(d)
(e)
(f)
Derivative (incr. rate)
Derivative (establish.)
Derivative (density)
(g)
(h)
(i)
Dissimilarity (derivatives)
Median = 1.13
Median = 2.11
Median = 2.05
Divergence
Flowering plant abundance
Grazing pressure
Fire frequency


(a)
Intrinsic rate of increase (r)
(b)
Carrying Capacity (log10K)
T. pyriformis
Loxocephalus sp.
C. striatum
P. caudatum
(c)
Derivative (r)
(d)
Derivative (log10K)
(e)
Dissimilarity (derivatives)
Median = 1.18
(f)
Dissimilarity (derivatives)
Median = 1.07
Divergence
Divergence
Temperature (°C)
Temperature (°C)


(a) Intrinsic rate of increase (r)
(b) Carrying capacity (log10K)
Relationship with community stability (model slope)
0.10
0.05
0.00
−0.05
Correlation
(Dis)similarity
Divergence
Correlation
(Dis)similarity
Divergence
Response diversity metric