Response diversity in the context of multifarious environmental change

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# Abstract

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# Introduction

Ecological stability concerns responses of ecosystems and their components to environmental change (Pimm 1984; Mccann 2000; Donohue *et al.* 2013). A stable population, community, or ecosystem will change less than a less stable or unstable one. Greater stability can mean lower chance of population extinction (citation), lower variability of an aggregate property such as total community biomass (citation), and lower variability of ecosystem processes (citation). All of these can promote ecological sustainability (citation). It is perhaps unsurprising then that stability has occupied a central place in ecological research for decades.

Ecological stability is a multidimensional concept, with components such as resilience, resistance, persistence, robustness, and variability (Donohue et al). One particularly relevant component is the temporal variability (or temporal stability) of aggregate properties, such as total community biomass (Hautier *et al.* 2015). Low temporal variability is associated with predictable and sustainable delivery of ecosystem functions (Elmqvist *et al.* 2003; Renard & Tilman 2019). It is this component of ecological stability that we are primarily concerned with in this paper.

There is a general consensus that biodiversity dampens variability in aggregate community and ecosystem properties (Hautier *et al.* 2015; Isbell *et al.* 2015). This is because, in species rich communities, there is a higher chance that a reduction in abundance or performance of one species may be compensated for by an increase in abundance or performance of another species (Yachi & Loreau 1999). Such dynamics have been named compensatory or asynchronous, and have been broadly identified as the main driver of temporal stability (Gonzalez & Loreau 2009; Craven *et al.* 2018; Sasaki *et al.* 2019).

Compensatory dynamics can happen by chance, and when there are more species present then the chances of compensatory dynamics can increase (Yachi and Loreau 1999). Compensatory dynamics can also happen when species differ in their responses to environmental conditions (McCann 2016). When environmental conditions are changing over time, as it is common in natural systems, communities composed of species differing in their responses to the environment may maintain stable levels of aggregate properties over time through asynchronous (compensatory) fluctuations (Mori *et al.* 2013). This element of biodiversity is.

The stabilising effects of response diversity have good theoretical foundations. For example, Ives et al. (1999) showed that differences in how species respond to environmental change (response diversity) may determine community stability. Using a modelling approach of randomly constructed competitive communities, Ives and Carpenter (2007) found that response diversity is the most significant driver of temporal stability, outweighing the destabilising effects of interspecific interactions. These findings suggested that it is not biodiversity *per se* that enhances stability, but rather the diversity of species responses to the environment. That is, response diversity may be the ecological mechanism (although perhaps not the only one) producing the insurance effect of biodiversity (Yachi & Loreau 1999), and determining asynchronous population dynamics in changing environments (Downing *et al.* 2008).

Despite its intuitive relevance as driver of temporal stability, evidence classifying response diversity as fundamental mechanism dampening temporal variability in communities is currently lacking, as there has been no systematic attempt to quantify its role in this context.

The lack of extensive investigations on whether response diversity is the main driver of temporal variability of aggregate community properties mainly relates to the absence of a standardised and consistent ways to quantify response diversity. The limited studies that have measured response diversity have done so in different ways (Ross *et al.* 2023). For example (i) using low-level functional traits that forecast some feature of species response to the environment, such as clutch size or specific leaf area (Sasaki *et al.* 2019). Or (ii) by measuring species-specific interaction between environment and abundance in a community context, where if species show different abundance – environment relationship, they have response diversity (Winfree & Kremen 2008). Or, else, (iii) measuring some aspect of a population's performance, such as its intrinsic rate of increase (McCann 2016) or biomass change in response to the environment, and taking the range of performance–environment model slopes as a direct estimate of response diversity (Leary & Petchey 2009). Lately, (iv) response diversity has also been quantified using ecological network analysis of traits, where a higher network complexity represents higher response diversity (Gladstone-Gallagher *et al.* 2023).

Recently, a new approach has been developed to empirically quantify response diversity (Ross *et al.* 2022). The approach of Ross *et al*. (2022) is a flexible and robust method to study how species identity and diversity shape ecological stability in face of disturbance. It is based on species’ performance curves, e.g., how temperature affects growth rate, and can work with non-linear performance curves. Response diversity is then the variation in the slope of the performance curves. By capturing how species’ performances depend on their environmental context, this new response diversity framework allows testing the diversity-stability relationship from a new perspective and represents a new tool to mechanistically understand such relationship in a new, standardised way (Ross et al 2023).

Nevertheless, this framework has a significant limitation. It is not able to capture response diversity in the context of multiple simultaneously changing (multifarious) environmental drivers. This is particularly limiting as human activities have caused an increase in the number and intensity of anthropogenic drivers acting on ecosystems (IPCC-IPBES 2020). Multiple environmental drivers may affect ecosystems at a given point in time, potentially undermining their species diversity as well as their stability (Donohue *et al.* 2016; Zelnik *et al.* 2018). Thus, we need methods to quantify response diversity inthe context of multifarious environmental change.

Furthermore, a multifarious context raises potential for interactions between drivers, which may result in effects larger than (synergism) or smaller than (antagonism) those expected from the sum of the individual stressors (additive) (Piggott *et al.* 2015). Evidence shows that multiple interacting drivers are impacting ecosystem’s diversity and stability (Pires *et al.* 2018; Polazzo & Rico 2021), and meta-analyses summarising available research on multiple driver impacts have highlighted that non-additive effects are common (Crain *et al.* 2008; Jackson *et al.* 2016; Birk *et al.* 2020).

Yet, there has been little if any exploration of response diversity in the context of multiple simultaneously changing environmental drivers (multifarious environmental change). Hence, an extension of this method is urgently needed to understand whether response diversity is a key determinant of stability in communities exposed to multifarious environmental change. Understanding the role of response diversity in driving the diversity-stability relationship in face of multiple environmental drivers may help translating experimental results and theoretical advancements into information for policymakers due to the greater relevance of the multifarious context. Such information is important, as the temporal variability of aggregate properties plays a central role in human’s economy and food production (Armsworth & Roughgarden 2003; Renard & Tilman 2019), and contributes to several aspects related to human well-being (Cardinale *et al.* 2012).

Here, building on the method developed by Ross *et al.* (2023), we propose a newmethod to empirically quantify response diversity in the context of multifarious environmental change. We show its validity using simulated data representing species-environment performance curves in cases with and without interactions between environmental drivers. Next, we investigate the role of the direction of environmental change in shaping response diversity when multiple drivers of environmental change fluctuate over time. In this regard, we show that, when the direction of the environmental change is unknown (e.g. there are no information on how the environmental condition have changed or are going to change), we can quantify an “absolute” response diversity for a given community, providing useful information for multiple situations. Finally, we investigate the drivers of response diversity in a multifarious environmental change context, showing how response diversity depends on the diversity of species response to each of the environmental variables, on the relative effect of each environmental variable on species’ traits, and on the correlation between the diversity in species’ responses to different environmental variables.

# The principle and how to apply it

In this section we describe the new method to quantify response diversity in the context of multiple environmental variables. We start explaining the principle and the underlying mathematical concepts. Then, we describe how to calculate response diversity in two important and distinct situations: when the environmental conditions are known, and when the environmental conditions are unknown..

## The principle

Here, we propose an empirically tractable method for empirically quantifying response diversity in the context of multifarious environmental change that can be easily applied to experimental as well as observational studies.

Researchers have previously suggested that the response diversity of a community can be measured by the diversity of responses to environmental change (Mori *et al.* 2013; McCann 2016). Ross *et al.* (2023) proposed characterising species’ responses with the first derivative of their performance – environment function evaluated over an environmental gradient. By fitting individual species’ performance – environment relationship using GAMs, then taking the first derivative of the GAM to estimate the model slopes along the environmental axis, and finally measuring the variation of the first derivatives, they provide a flexible methodology to measure response diversity applicable when species responses are linear as well as non-linear.

For example, one can measure the response of each of the species’ intrinsic growth rate to temperature, quantify the strength and direction of these responses (e.g., as the first derivative of the response curve), and calculate the diversity of responses (e.g., by calculating variation in the first derivatives among the species in a community). When responses are nonlinear, the response diversity will be a function of the environmental state (i.e. the first derivative is a function of the value of the environmental state, maybe do a figure to visualise the concept?). This approach has been demonstrated to be suitable for quantifying response diversity in the context of a single environmental driver, but given that multiple environmental drivers can change simultaneously, an approach that works in that context is needed.

Imagine that the growth rate of a population depends on two environmental factors, e.g. temperature and salinity. Instead of a response *curve*, we have a *response surface*. We can represent the dependency as , where  is growth rate,  is temperature,  is salinity, and *f* is some function. It may be that the dependencies are linear, nonlinear, and with an interaction between temperature and salinity, hence our approach needs to be able to accommodate these phenomena.

The solution we developed is a relatively straightforward extension from 1-dimension to 2-dimensions of environmental change (and can in principle be extended further to many dimensions). Instead of calculating variation in the first derivative, we calculated variation in the *directional (first) derivative*. The *directional derivative* is the slope at a particular point on a surface in a particular direction.

Imagine standing on a hill. The slope depends on where you are on the hill (e.g. on a side, or at the top), and also the direction you face (e.g., up the slope, or along a contour). To find the directional derivative we must, therefore, specify a location on the surface and a direction on the surface. The mathematical calculation then involves calculating the *partial derivatives* at that location. The partial derivatives are the slope of the surface in the direction of change in only one, or other, of the predictors variables (e.g., along one predictor axis, or the other). The partial derivatives are then added together in proportion to the direction, to give the directional derivative.

To understand from a mathematical perspective, consider a response surface with growth rate as the dependent variable (the height of the surface) and temperature and salinity as the predictor variables. To calculate a directional derivative we give the location on the surface as , and the direction of environmental change is given by the unit vector . A unit vector has length 1, and is used because only the direction of change is important, and not the amount of change. Furthermore, let the two partial derivatives be  : the partial derivative of  with respect to , and  : the partial derivative of with respect to .

The directional derivative sis then given by

Efficient evaluation in *n* dimensions can be done by taking the dot product of the partial derivatives at the location and the direction unit vector:

Where, .

Diagram of a diagram of a temperature

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Figure 1. Illustration of the principle. The growth rate of a species is determined by changes in temperature and salinity. The slope of a point on the surface depends on the location on the surface (e.g. environmental location) and on the direction of the environmental change. The slope can depend on the location on the surface and the direction on the surface, and hence is termed the directional derivative. In the illustration, a particular case where temperature and salinity change by an equal amount is shown, as well as the case for the two partial derivatives.

## Calculating the partial derivatives

Following Ross *et al.* (2023), we use Generalized Additive Models (GAMs) to fit species’ response surfaces to multifarious environmental change and calculatd the partial derivatives of the GAM model.GAMs allow to fit response surfaces of the response variable using tensor-products. Tensor products are a mathematical way of representing joint interactions between several predictors (environmental driver variables) and are particularly suitable when predictors are measured on different scales. Furthermore, GAMs with tensor-products can fit response surfaces with interacting predictor variables..As mentioned, the first step to calculate a directional derivative (i.e. the slope on a surface) is to calculate its partial derivatives. Mathematically, a partial derivative of a function of multiple variables is its derivatives with respect to one of these variables, with the other variables held constant. A partial derivative with respect to a specific variable can be conceptualized as the rate of change of the function in the direction of the variable considered. Coming back to the above example, where the growth rate of a species is affected by temperature and salinity, the partial derivative with respect to temperature represents the change in growth rate as temperature changes, when salinity is held constant at a specific value. In other words, we analyse the effect of temperature change, along a slice of the response surface (Fig. 2).

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Figure 2. Calculation of the partial derivatives. (a and d) The response surface for a species. (a) The black solid line represents the value of salinity at which the partial derivative with respect to temperature is calculated. (b) The effect of temperature on the species’ growth rate when salinity is held constant at 20 ppt. (c) The calculated partial derivative with respect to temperature, when salinity is held constant at 20 ppt. (d) The black solid line represents the value of temperature at which the partial derivative with respect to salinity is calculated. (e) The effect of salinity on the species’ growth rate when temperature is held constant at 300 K. (f) The calculated partial derivative with respect to salinity, when temperature is held constant at 300 K.

## Directional derivatives

Directional derivatives are given by summingthe partial derivatives when they are weighted by the direction. Intuitively, a directional derivative describes the rate of change of a function at a particular point in a defined direction (i.e. change in the growth rate of a species as multiple environmental variables change). Calculating a directional derivative, therefore, requires knowing the direction, and this is encoded in a unit vector (i.e. the direction in which the directional derivative is been calculated). The direction in which the directional derivative is calculated can be arbitrary, but in an ecological context, the direction will be dictated, in most cases, by the trajectory of change in the environmental conditions over time.

Translating this into our example, to calculate the slope (directional derivative) of a point on the response surface (a species’ response to changes in temperature and salinity), we need to know the location on the surface (environmental location) and the direction of change in the environment (how the environmental drivers change over time). The direction of change in the environment can be derived from time-series, where one could track how multiple environmental variables change over time, or from predictions about how the environment will change in the future. Yet, there may be several cases when the direction of environmental change is unknown, but one may be nonetheless interested in calculating response diversity. We are now going to analyse these two cases separately.

## Known direction of environmental change

If the direction of the environmental change is known then calculatingdirectional derivatives is straightforward and proceeds exactly as described above. For example, in Fig. 3, we can see that temperature increases as we move from time 0 to time 1 (Fig. 3a), whereas salinity decreases in the same time interval (Fig. 3b). Plotting this trajectory of environmental change on a species’ response surface (Fig. 3c) will give us a visual representation of the direction in which the directional derivative is calculated when we follow the direction of the environmental change. As the environmental conditions change from T0 to T1 on the species’ response surface, the trajectory traverses an area of the surface where the species’ growth rate increases. Intuitively, this should result in a positive slope when the environment changes from 0 to 1. Calculating the directional derivative indeed results in a positive value of the directional derivative (Fig. 3d).

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Figure 3. Calculation of the directional derivative. (a) Change in temperature from T0 to T1. (b) Change in salinity from T0 to T1. (c) Direction of the environmental change over time displayed on the species' response. (d) Directional derivative change from T0 to T1.

When dealing with a time series, we have multiple time points, and environmental conditions change as time passes. In this situation, one only needs to repeat the steps illustrated above for all the time points of the time series (Fig. 4).

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Figure 4. Calculation of directional derivatives for one species for a time series of environmental change. (a) Time series of temperature change. (b) Time series of salinity change. (c) Direction of the environmental change over time displayed on the species' response surface. (d) Directional derivative values over time.

In a community context, one can calculate the directional derivative over time in the direction of the environmental change for each individual species. Next, by applying the approach of Ross *et al.* (2023), one can measure the variation in the directional derivatives of the species composing a community as dissimilarity and divergence, the two metrics proposed to quantify response diversity (Fig. 5).

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Figure 5. Response diversity calculation. (a-d) Response surface of the species composing the community with the direction of the environmental change displayed on the surfaces. (e) Directional derivatives of the species over time. (f) Response diversity calculated as dissimilarity. (g) Response diversity calculated as divergence.

## Unknown direction of environmental change

The direction of change in environmental conditions may be unknown in multiple situations. Probably, the most obvious case is when one is dealing with future predictions, and there is high uncertainty about how the environment is going to change. Yet, there might be several other cases when one may want to know response diversity without knowing the direction of the environmental change. Consider the case where one only has data about species performances collected in only few environmental contexts (i.e. laboratory factorial experiments) but wants to assemble communities differing in composition and expose them to different environmental change scenarios. Knowing the response diversity of these communities with unknown direction of environmental change would be extremely useful to test a variety of different ecological questions. In this section, we are going to explore a possible way to calculate response diversity when the direction of the environmental change is unknown, by quantifying response diversity to all possible environmental changes and taking the average.Let us consider one environmental location on the response surface of a species, whose growth rate is, again, determined by changes in temperature and salinity. As we do not know how the environmental drivers are going to change, we can calculate the directional derivative for that particular point in many possible directions (Fig. 6).

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Figure 6. Directional derivatives calculated in many directions for a point on one species' response surface.

We can do the same for a grid of points covering the whole response surface, for all the species composing a given community. Then, we calculate the diversity in the directional derivatives across the whole surface (all environmental locations) across all species in a particular direction. We subsequentially repeat the same operation in all possible directions. Finally, the mean value of the calculated diversity in all possible directions gives us a response diversity value for a community (Fig. 7).

To be clear, the steps to calculate the absolute response diversity can be summarised as follow:

1. Calculate every , that is the directional derivative of each species in each location in each direction.
2. Calculate , that is, the diversity of the directional derivatives for a location and direction across species.
3. Calculate , that is the average diversity across locations and directions.

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Figure 7. Illustration of the principle underlying the calculation of absolute response diversity. Considering the difficulties related to displaying multiple 3D response surfaces, each having multiple points with directional derivatives going in all possible directions, we focus here in representing only two species and nine points on each surface. For those points, we only display three directional derivatives to help the reader visualising the calculation process, but please note that computationally this is done for many points and many directional derivatives.

Response diversity when the direction of environmental change is unknown could be used for systematically measuring response diversity to all potential environmental changes. It represents the potential response diversity, which captures the complete insurance capacity of a system under all possible environmental conditions.Absolute response diversity can be seen as a more comprehensive quantification of response diversity that does not depend on the direction of the environmental change. Even though here we quantify it in a two environmental drivers context, it can be calculated for cases where more than two drivers influence species traits. Its application is potentially very broad. Absolute response diversity can be used to assemble communities having the highest possible response diversity to all potential directions of environmental change, providing a way to maintain functional levels as stable as ecologically possible. This option opens the door to a wide array of applied purposes of absolute response diversity, from industrial/production scopes to conservation actions. Being able to assemble communities specifically designed to have high absolute response diversity can allow ecosystem managers to buffer the negative effects of environmental change on ecosystem functioning in specific situations but may also be used to test relevant ecological questions. Indeed, having a way to quantify absolute response diversity allows scientists to assemble communities with different levels of absolute response diversity. Communities assembled along a gradient of absolute response diversity could then be used to directly test the link between response diversity and community temporal stability, providing a new way to get insight on whether response diversity mechanistically drive temporal stability that does not depend on the environmental change scenario.

# Testing the principle and investigating the drivers of response diversity

In this section we apply the method previously introduced using simulated species responses to two environmental drivers. For consistency we continue with the example of species influenced in their growth rate by temperature and salinity. Next, we investigate various drivers of response diversity in a multifarious environmental change context, highlighting what those drivers are and how they act influencing response diversity.

## Simulating species responses to environmental change

To test our methodological advancement, we simulated species growth rate under the influence of two environmental drivers. Numerous mathematical functions have been used to represent how organismal performance changes with an environmental driver (citation require). Moreover, multiple mathematical functions have been used to represent an interactive effect of two or more environmental drivers on species performance (e.g. Thomas *et al.* 2017).

For its widespread application and ease of implementation, we used here the Eppley equation (Formula 1: Eppley, 1972).

Where is the value of the environmental factor, controls the location of the maximum, controls the range of (environmental driver) over which the rate is positive, is a scaling constant, and controls the rate of increase towards the maximum rate as increases.

The original Eppley function was developed to simulate species response to only one environmental variable. We thus adjusted it here to be able to account for the effects of two environmental drivers on species responses.

Species often show stronger responses to one particular driver compared to another one, even when the overall response is mediated by more than one driver of environmental change (Schulhof *et al.* 2019). This is, the growth rate of a species increases or decreases more in response to a given change in one environmental variable compared to the same amount of change in another environmental variable. To specifically simulate this kind of behaviour, we introduced differences in the magnitude of responses to different environmental variables by setting different values for the parameters *a* and *b*, so that temperature would be the environmental variable having the largest effect on species’ growth rate (Fig. 8a, b).

= 1e-9,

= 0.063,

= 285,

= 60,

= 1e-3,

= 0.02,

= 20,

= 10

Additionally, we included interactions between the two environmental variables making the value of at which the rate is maximised depend on the value of :

The interaction term allows us to easily insert an interactive environmental effect. When , eq 3 becomes the previously mentioned eq 2 (additive effect). When , then the value of (i.e. temperature) at which the rate is maximised is a function of the value of (i.e. salinity) (Fig. 8c, d). We used this method for adding an interaction due to its simplicity of implementation, but our method should be robust and should work with other approaches as well.

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Figure 8. Simulated species responses to changes in temperature and salinity. (a-b) Additive species responses. (c-d) Interactive environmental effect on species response.

## Drivers of response diversity in a multifarious environmental change context

We hypothesised that multiple factors may shape response diversity in a multifarious environmental change context. Specifically, we investigated whether the three following factors may drive response diversity:

1. The relative strength of effect of different environmental drivers.
2. Correlation in species' responses to different environmental drivers.
3. Mean value of environmental conditions.

Factor I. In the previous section, we specified that we set the parameters of Eqn. 2 so that salinity has a relatively large effect on on species’ growth rate compared to the effect of temperature. Yet, this may not be always the case for all species. For example, there might be species and communities in which species are quite equally influenced by multiple environmental variables. To explore whether and how response diversity is influenced by relative effects sizes of different environmental variables, we simulated another case where species are equally influenced in their growth rate by temperature and salinity (Fig. 9). Using this different type of response surfaces, we created the same communities and scenarios of diversity in species’ responses and correlation between diversity in responses to salinity and temperature created in the previous step.

A graph of different types of temperature

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Figure 9. Simulated species responses to changes in temperature and salinity, where salinity and temperature have the same effect on species’ growth rate. (a-b) Additive species responses. (c-d) Interactive environmental effect on species response.

Factor II.Species in a community may show high diversity in how they respond to one of the drivers, but very little variation in how they respond to a second (and third, fourth, etc.) environmental driver. Alternatively, species could show high diversity in response to all environmental drivers. To test whether and how the diversity in species’ responses to the environment in a multi-driver context shape response diversity, we varied species responses to one (i.e. only temperature), or both (i.e. temperature and salinity), environmental drivers in different combinations.

The differences in species responses were introduced by changing the amount of variation (diversity) across species in the position of the optimum growth rate for each driver within a community (Fig. 10a, b, c). Thus, a community composed of species having very different optimum values for one driver (i.e. temperature) will show high diversity in responses to changes in that driver.

We simulated three different scenarios. In the first one (Fig. 10d), we created three communities of ten species that vary in the amount of diversity in responses to only one environmental driver (e.g. temperature), whereas the diversity in responses to the second environmental driver (e.g. salinity) was kept fixed at an intermediate value. In the second scenario (Fig 10e), we created three communities having increasing diversity in responses to both drivers, so that community 1 had low diversity in responses to temperature and salinity, community 2 had intermediate diversity in responses to temperature and salinity, and community three had high diversity in responses to temperature and salinity. In this second scenario, the diversity in responses to the two environmental drivers increases with positive correlation (when diversity in species’ responses to temperature increases, so does diversity in species’ responses to salinity) across the community. Thus, we called this the positive correlation in diversity scenario.

In the last scenario (Fig. 10f), we created three communities where the diversity in species’ responses to one driver (i.e. temperature) increases, the diversity in species’ responses to the other variable (i.e. salinity) decreases, and vice versa. Hence, community 1 has high diversity in responses to salinity, but low to temperature. Oppositely, community 3 has high diversity in responses to temperature, but low to salinity. Community 2 represents an intermediate case where both the diversity in responses to temperature and salinity are moderate. We called this the negative correlation in diversity scenario.

For these first two factors (I. relative strength of driver effects and II. correlation of diversity) we calculated absolute response diversity of each community.

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Figure 10. Varying diversity in species’ responses to salinity and temperature. (a-c) Conceptual illustration of increasing diversity of species' response to temperature. (d-f) Different simulated scenarios of correlation between diversity in species' responses

|  |  |
| --- | --- |
| Scenario | Diversity pattern across communities |
| 1 | Communities differ only in diversity of T\_opt; diversity of S\_opt held constant across communities. |
| 2 | Communities differ in diversity of T\_opt and S\_opt, but in a positively correlated fashion. |
| 3 | Communities differ in diversity of T\_opt and S\_opt, but in a negatively correlated fashion. |



Factor III. When response curves are nonlinear then the derivatives and hence response diversity depends on the value of the environmental driver. Hence, the mean value around which each environmental variable fluctuates can be a major determinant of response diversity. Let us consider the example of a community composed of species having very little diversity in the optimum positions for an environmental variable (i.e. temperature). In this case, independently of the mean value of the environmental variable, the species in the community will show very similar responses (Fig. 11g).

In an contrasting situation, where the species composing a community have high diversity in the values of the optimum for an environmental variable, the mean value around which the environmental variable is fluctuating may have a large impact on the diversity of responses showed by the species in this community (Fig 11i). Yet, when the species responses depend on multiple environmental drivers, how much the mean value of one of those drivers influences the overall response diversity will be dependent on the mean value of the other environmental drivers, and on the diversity in responses of the species to each of the drivers (i.e., will depend on just about everything!!!).

To quantify the effect of the mean value of the environmental drivers on multifarious response diversity, we combined the different scenarios of variation and correlation in species' responses to the environment, in the cases where temperature has larger effect on growth rate as well as in the cases where temperature and salinity equally influence species’ growth rate, changing the mean value around which temperature and salinity fluctuate. This resulted in three additional scenarios of mean value of environmental conditions: low mean value, where both temperature and salinity fluctuate around low mean values; intermediate scenario, where temperature and salinity fluctuate around intermediate mean values; and high mean scenario, where temperature and salinity fluctuate around high mean values.

We anticipated that the higher response diversity should be found for communities having high diversity in responses to both salinity and temperature exposed to environmental change fluctuating around intermediate mean values. This is because, when temperature and salinity fluctuate around intermediate values in a community with high diversity in responses (very different optimum positions along the environmental gradient) to both environmental variables, the fluctuations lie on the left of some response curves (surfaces) and on the right of others (Fig. 11i). Indeed, such community will be composed of some species having high optimum values for temperature and salinity, others having low optimum values for temperature and salinity, others having high optimum values for salinity, but low for temperature or vice versa. Hence, only when the environmental drivers fluctuate with intermediate values, all the diversity in responses can be captured. However, differences in the value of response diversity are expected depending on whether temperature is the main environmental variable influencing species’ growth rate or whether both environmental variables have the same effect on growth rate.

A collage of graphs and diagrams

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Figure 11. Variation in the mean value of the environment and its relationship with diversity of species' optimum positions. (a-b) Temperature and salinity fluctuate with low mean values. (c-d) Temperature and salinity fluctuate with intermediate mean values. (e-f) Temperature and salinity fluctuate with high mean values. (g-i) Increasing diversity in species’ optimum positions. Shaded areas in different colours show the intervals in which temperature is fluctuating depending on it mean value scenarios.

We simulated all the scenarios and combinations described above for additive and interactive environmental effects on species’ responses. However, no qualitative difference was found. We thus report only the results obtained using the additive effect.

## Effects of variation in species' responses to the environment on absolute response diversity

The diversity in species’ responses to the environmental variables (Factor I), created introducing variation in species’ optimum positions for one, or both variables was found to be a major driver of absolute response diversity (Fig. 12). However, the effect of the diversity in species’ responses to temperature and salinity strongly depended on whether temperature was the strongest environmental driver, or whether temperature and salinity equally affected species growth rate (Factor II).

When temperature was the dominant driver of species’ growth rate, dissimilarity was always higher in communities having high diversity in species’ responses to temperature, irrespective of whether diversity in species’ responses to salinity was high, intermediate, or low. Conversely, when temperature and salinity equally influenced species’ growth rate, functional dissimilarity was high only when responses to both temperature and salinity were high. When only either diversity to salinity or to temperature was high, functional dissimilarity had intermediate values, where it was lowest when diversity in species’ responses to temperature and salinity was low.

Similarly, divergence was consistently higher in communities characterised by high diversity in the position of the optimum for temperature, when temperature was the dominant environmental driver. The highest value of divergence in this case was found for the community having high diversity in optimum position for both temperature and salinity. The lowest divergence value was found for the community having low diversity in optimum position for temperature and salinity. In this case, divergence was also high when only diversity in species’ responses to temperature was high, but low in responses to salinity.

When temperature and salinity had the same strength of effect on species’ growth rate, divergence was highest when both diversity in species’ response to salinity and temperature were high. The second highest divergence value was found for the community having high diversity in species’ responses to temperature and intermediate to salinity. In contrast to the case where temperature was the dominant environmental driver, communities having high diversity in species’ responses to only one of the environmental drivers had intermediate values of divergence. Again, the lowest divergence value was found for the community having low diversity in optimum position for temperature and salinity (Fig 12b).

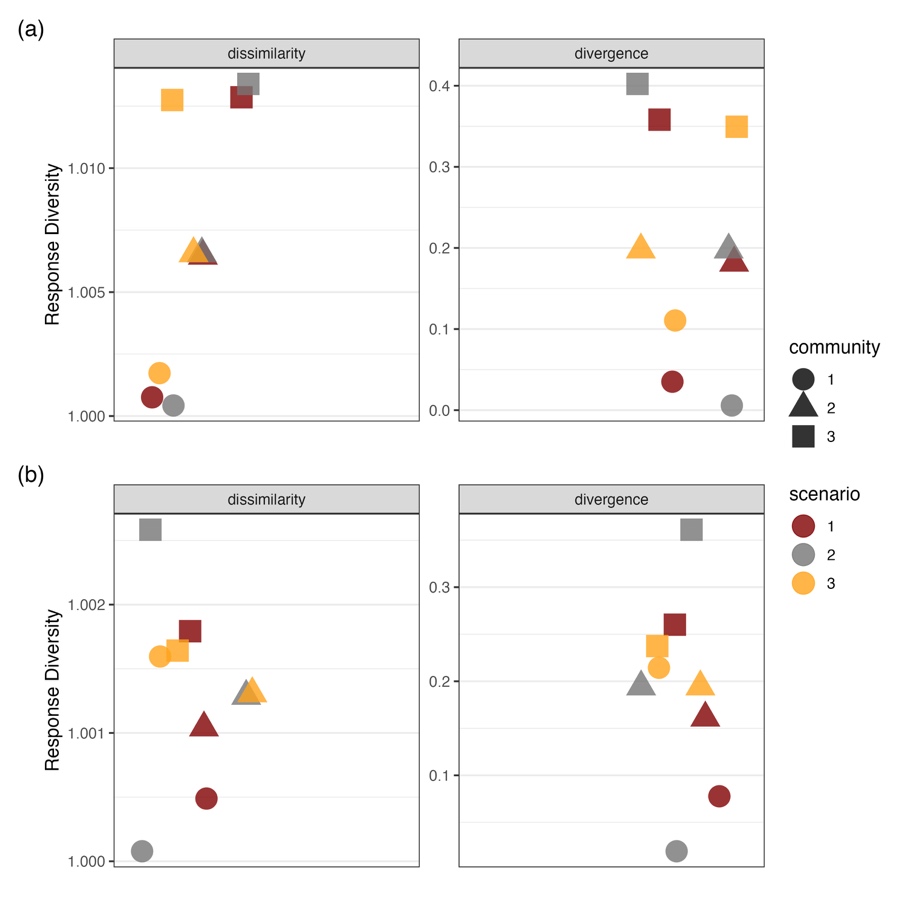


Figure 12. Absolute response diversity. Absolute response diversity measured as dissimilarity and divergence colour coded based on the different scenarios of diversity in species' responses. Different shapes indicate different communities within the same diversity scenario. (a) Shows absolute response diversity for the case where temperature has a larger effect on species’ growth rate compared to salinity. (b) Shows absolute response diversity for the case when temperature and salinity have the same effect on species’ growth rate.

## Effects of mean value of environmental variables on response diversity

The mean value around which temperature and salinity fluctuated had a large impact on response diversity, independently of whether it was measured as dissimilarity or divergence. Though, the patterns showed by the two different metrics differed substantially, and, for divergence, it also depended on whether temperature was the dominant environmental driver.

Dissimilarity increased gradually with the increase in diversity of temperature optimum, independently on whether temperature was the dominant environmental driver or whether temperature and salinity had an equal effect. The highest value was always found for communities having high diversity in species’ response to temperature and exposed to environmental conditions characterised by high mean value (Fig 13). There was not qualitative difference in dissimilarity trends between the different scenarios of correlation between diversity in optimum position to the environmental drivers when temperature was the dominant environmental driver.

When temperature and salinity had the same effect on species’ growth rate, dissimilarity showed the same trends. The only exception was represented by the negative correlation in optimum diversity scenario, which showed similar level of dissimilarity when the diversity of species’ responses to only one of the environmental variables was high, and the other low. Again, though, the highest dissimilarity was always found for communities exposed to temperature and salinity fluctuating around high mean values.

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Figure 13. Effects of diversity in species’ responses on response diversity measured as dissimilarity. (a), (b), and (c) show how dissimilarity changes in the different scenarios of correlation between temperature and salinity optimum diversity depending on the mean value of the environment in the case where temperature is the dominant variable. (d), (e), and (f) show how dissimilarity changes in the different scenarios of correlation between temperature and salinity optimum diversity depending on the mean value of the environment in the case where temperature and salinity have an equal effect on species’ growth rate.

Divergence also increased with increasing diversity of species’ temperature optimum, but the highest values were consistently found for communities exposed to temperature and salinity fluctuating around intermediate mean values. The only exception to this consistent trend was represented by communities having fixed intermediated diversity in species’ responses to salinity and increasing to temperature when salinity and temperature had an equal effect on species’ growth rate. Those communities showed always higher response diversity when exposed to temperature and salinity fluctuating around low mean values (Fig. 14d).

The scenario where species had low diversity in optimum position for both temperature and salinity showed the lowest divergence values (Fig 14b and e), independently of the mean value of the environmental variables, and independently of whether temperature was the dominant environmental driver or whether temperature and salinity had an equal effect.

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Figure 14. Effects of diversity in species’ responses on response diversity measured as divergence. (a), (b), and (c) show how divergence changes in the different scenarios of correlation between temperature and salinity optimum diversity depending on the mean value of the environment in the case where temperature is the dominant variable. (d), (e), and (f) show how divergence changes in the different scenarios of correlation between temperature and salinity optimum diversity depending on the mean value of the environment in the case where temperature and salinity have an equal effect on species’ growth rate.

## Discussion on the drivers of absolute multifarious response diversity

Our work based on simulated species responses to multifarious environmental change suggests that the diversity of species’ responses to each of the environmental variable is a nuanced, but major driver of absolute response diversity.

Dissimilarity, when temperature was the main environmental driver, was consistently higher in community three of all three scenarios. This result is particularly meaningful for scenario 1, where diversity in the optimum values is maximum for temperature, but fixed across the different communities for salinity, and the positive correlation in optimum diversity scenario, where the diversity in optimum values is maximum for both temperature and salinity. In these two cases, response diversity was expected to increase, at thus the results are not surprising. Yet, dissimilarity was high also in community three of the negative correlation in optimum diversity scenario (high diversity in species’ responses to temperature, but low to salinity). **This finding suggests that, when species’ responses are more strongly influenced by one environmental variable compared to another one, having high diversity in responses to the dominant environmental variable is sufficient to determine high dissimilarity.** **Conversely, a community characterised by high diversity in responses to salinity, but low to temperature, will result in lower dissimilarity in this case, as shown by community one of the negative correlation in optimum diversity scenario**. Such community showed dissimilarity level similar to community one of the positive correlation in optimum diversity scenario, which is characterised by low diversity in species’ responses to salinity and temperature. However, this is not the case when salinity and temperature had the same effect on species growth rate. In this case, communities having high diversity in species’ responses to only one of the two drivers had intermediate dissimilarity values. When temperature and salinity had the same effect, high dissimilarity was only showed by the community characterised by high diversity in species’ responses to both environmental drivers.

Divergence, showed clear and meaningful patterns as we manipulated the diversity of species responses to one or both environmental variables. Intuitively, one would expect response diversity to increase along with the increase in diversity of species’ responses, with the maximum response diversity exhibited by communities having the highest variation possible in species’ responses to all environmental variables. Our findings align with these expectations, and the simulated community composed of species with high diversity in responses to temperature and salinity showed the highest absolute divergence. Although perhaps not surprising, this result provided us with support that our approach to quantify absolute response diversity is meaningful and grounded on theoretical basis.

We initially simulated a case where species’ growth rates were more strongly influenced by temperature than salinity. We introduced differences in the magnitude of responses to the environmental variables as generally species responses may be more affected by certain environmental drivers than others (Schulhof *et al.* 2019). Yet, we acknowledged that this may not be always the case for all species. For example, some species may be more affected in their growth rate by salinity than temperature, or temperature and salinity may have the same effect on species’ growth rate. We thus wanted to investigate whether and how response diversity changes in communities composed of species whose growth rate is equally influenced by temperature and salinity, compared to the case where temperature is dominant environmental variable in influencing species’ growth rate. Put differently, we investigated whether differences in the relative influence of environmental variables on species’ traits may determine different values of response diversity. We indeed found differences between these two cases.

For instance, absolute response diversity measured as divergence, was found to be higher for a community having high diversity in species’ optimum positions for temperature, but low diversity for salinity, compared to a community having high diversity in species’ optimum positions for salinity, but low for temperature (Fig. 12). When we simulated the same example, but this time species had exactly the same response curves to salinity and temperature (e.g. salinity and temperature have the same effect on species’ growth rate), the absolute divergence was the same in the two scenarios (Fig 12). **Hence, response diversity is influence not only by the diversity in species responses to each of the environmental variable, but also by the relative impact of the environmental variables on the trait used to quantify response diversity.**

This was also particularly clear when looking at absolute functional divergence of the community three of the negative correlation in optimum diversity scenario (high diversity in species’ responses to temperature, but low to salinity), which showed a higher value compared to communities two of the first, second, and third scenarios (all showing intermediate species’ diversity in response to both salinity and temperature). This seems to suggest that having high diversity in species’ responses to one environmental driver, but low to another one, leads to higher absolute dissimilarity compared to having intermediate diversity of species’ responses to both environmental drivers. However, this is again determined by the stronger response species show to temperature. When species are equally influenced by two environmental variables, there is actually no qualitative difference in absolute divergence between the two scenario exposed above (high:low vs intermediate:intermediate, Fig 12). Overall, we highlight here the dependence of response diversity not only on the diversity in species’ responses to the single environmental variables, but also on the magnitude of the response species show to each environmental variable.

## Discussion on the effects of mean value of environmental variables of multifarious response diversity

The mean value around which the environmental variables fluctuate was found to be an important driver of response diversity. We anticipated that the highest response diversity should have been found when temperature and salinity fluctuate around an intermediate mean value in communities having high diversity in species’ responses to both environmental variables.

This expectation was not met for response dissimilarity. Dissimilarity was found to be consistently higher when temperature and salinity were fluctuating around high mean values, independently on whether temperature was the dominant environmental driver or not. Yet, this is easily explained by the shape of species’ response curves, which showed the largest magnitude of change in growth rate in response to either temperature or salinity at the higher end of the gradients (supplement figure). That is, species show (mostly) large and negative growth rate values at high values of salinity or temperature compared to the rest of gradient. Though, when diversity in species’ responses increases, even a less negative growth rate in the high end of the gradient for one of the two environmental variables results in a large value of dissimilarity. It is worthwhile remembering that dissimilarity does not consider the direction of the variation in the derivative values, but only considers the absolute variation. Hence, even if most of the responses have the same direction (negative growth rates, and thus negative derivatives), but one or few species in a community show less negative growth rate, this is sufficient to determine a high dissimilarity value.

Additionally, when species were more strongly influenced by temperature than salinity dissimilarity was found to be consistently higher in communities with high diversity in species’ responses to temperature, even when diversity in response to salinity was low, when temperature was fluctuating around a high mean value, compared to communities characterised by high diversity in species’ response to salinity, but low to temperature. Oppositely, when species’ growth rates were equally influenced by temperature and salinity, communities composed of species having low diversity in responses to temperature, but high to salinity, displayed dissimilarity as high as communities composed of species having low diversity in responses to salinity, but high to temperature (Fig 13). **Therefore, even when considering the direction of the environmental change, the relative magnitude of the impact of the environmental variables on species’ traits is a fundamental driver of response diversity.** In the case of dissimilarity, the different effect of the environmental variables on species’ growth rate was found to be more important than the mean value around which the environmental variable fluctuate.

Divergence, on the other hand, met our predictions. Divergence was always higher in communities characterised by high diversity in species’ responses to temperature, with the highest values consistently found when the environmental variables were fluctuating around intermediate mean values. This pattern was consistent in the case where temperature was the dominant driver, as well as in the case where temperature and salinity had the same effect in species’ growth rate.

The only exception was represented by communities having fixed intermediated diversity in species’ responses to salinity and increasing to temperature when salinity and temperature had an equal effect on species’ growth rate. Those communities showed always higher response diversity when exposed to temperature and salinity fluctuating around low mean values. This trend is determined by the fixed amount of variation in species’ responses to salinity. Indeed, the optimum position for all the species in this scenario falls within intermediate to low values of salinity. Thus, when salinity and temperature are fluctuating around a high mean value, response diversity is minimum, as all species have negative growth rate with respect to salinity. Oppositely, when salinity and temperature fluctuate with an intermediate mean value, most species have a positive growth rate with respect to salinity. When salinity and temperature fluctuate with a low mean value, most species have a negative growth rate, but some have a positive one to salinity, which results in the scenario having the highest diversity in responses, and thus highest divergence. Critically, this result only appears when salinity and temperature have the same effect on species’ growth rate. When temperature is the dominant driver, this effect is masked by the larger influence of the effects of temperature on divergence. Therefore, divergence appears to be at least equally influenced by the mean value around which the environmental fluctuate, and by the relative influence of each environmental driver on species’ traits.

Overall, divergence emerged as the most sensible measure of response diversity, showing meaningful and consistent patterns to our manipulations to diversity in species’ responses and to the variation of mean environmental values, without a strong dependence on the shape of species’ response curves.

# Conclusions and discussion

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# References

Anderegg, W.R.L., Konings, A.G., Trugman, A.T., Yu, K., Bowling, D.R., Gabbitas, R., *et al.* (2018). Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, 561, 538–541.

Armsworth, P.R. & Roughgarden, J.E. (2003). The economic value of ecological stability. *Proceedings of the National Academy of Sciences*, 100, 7147–7151.

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.E., Argillier, C., *et al.* (2020). Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology & Evolution*.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486.

Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.

Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., *et al.* (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nat Ecol Evol*, 2, 1579–1587.

Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., *et al.* (2016). Navigating the complexity of ecological stability. *Ecology letters*, 19, 1172–1185.

Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., Mcnally, L., Viana, M., *et al.* (2013). On the dimensionality of ecological stability. *Ecology Letters*, 16, 421–429.

Downing, A.L., Brown, B.L., Perrin, E.M., Keitt, T.H. & Leibold, M.A. (2008). Environmental Fluctuations Induce Scale-Dependent Compensation and Increase Stability in Plankton Ecosystems. *Ecology*, 89, 3204–3214.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., *et al.* (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1.

Gladstone-Gallagher, R.V., Hewitt, J.E., Siwicka, E., Gammal, J.M., Brustolin, M.C., Norkko, A., *et al.* (2023). Ecological network analysis of traits reveals variable response capacity to stress. *Proceedings of the Royal Society B: Biological Sciences*, 290, 20230403.

Gonzalez, A. & Loreau, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics*, 40.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T. & Reich, P.B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, 348, 336–340.

IPCC-IPBES. (2020). *Biodiversity and Climate Change: Scientific outcome*. *Ipbes-Ipcc Co-Sponsored Workshop*.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., *et al.* (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.

Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22, 180–189.

Leary, D.J. & Petchey, O.L. (2009). Testing a biological mechanism of the insurance hypothesis in experimental aquatic communities. *Journal of Animal Ecology*, 78, 1143–1151.

Mccann, K.S. (2000). The diversity–stability debate, 405.

McCann, M.J. (2016). Response diversity of free-floating plants to nutrient stoichiometry and temperature: growth and resting body formation. *PeerJ*, 4, e1781.

Mori, A.S., Furukawa, T. & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, 88, 349–364.

Piggott, J.J., Townsend, C.R. & Matthaei, C.D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution*, 5, 1538–1547.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

Pires, A.P.F., Srivastava, D.S., Marino, N.A.C., MacDonald, A.A.M., Figueiredo-Barros, M.P. & Farjalla, V.F. (2018). Interactive effects of climate change and biodiversity loss on ecosystem functioning. *Ecology*, 99.

Polazzo, F. & Rico, A. (2021). Effects of multiple stressors on the dimensionality of ecological stability. *Ecology Letters*, 1–13.

Renard, D. & Tilman, D. (2019). National food production stabilized by crop diversity. *Nature*, 571, 257–260.

Ross, S.R.P., Ross, S.R.P., Petchey, O.L., Sasaki, T. & Armitage, D.W. (2022). How to measure response diversity. *bioRxiv*, 1–29.

Ross, S.R.P.-J., Petchey, O.L., Sasaki, T. & Armitage, D.W. (n.d.). How to measure response diversity. *Methods in Ecology and Evolution*, n/a.

Sasaki, T., Lu, X., Hirota, M. & Bai, Y. (2019). Species asynchrony and response diversity determine multifunctional stability of natural grasslands. *Journal of Ecology*, 107, 1862–1875.

Schulhof, M.A., Shurin, J.B., Declerck, S.A.J. & Van de Waal, D.B. (2019). Phytoplankton growth and stoichiometric responses to warming, nutrient addition and grazing depend on lake productivity and cell size. *Global Change Biology*, 25, 2751–2762.

Thomas, M.K., Aranguren-Gassis, M., Kremer, C.T., Gould, M.R., Anderson, K., Klausmeier, C.A., *et al.* (2017). Temperature–nutrient interactions exacerbate sensitivity to warming in phytoplankton. *Global Change Biology*, 23, 3269–3280.

Winfree, R. & Kremen, C. (2008). Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B: Biological Sciences*, 276, 229–237.

Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 1463–1468.

Zelnik, Y.R., Arnoldi, J.F. & Loreau, M. (2018). The Impact of Spatial and Temporal Dimensions of Disturbances on Ecosystem Stability. *Frontiers in Ecology and Evolution*, 6.