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Stressor interactions at the community level: explaining qualitative mismatches between observations

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Article Type: Letter
Running Title: Stressor interactions at the community level
Keywords: Multiple Stressors, Non-Additivity, Antagonism, Synergism, Community Metrics, Richness, Hill Diversity, Multi-functionality

Abstract word count: 141
Main text word count: 3608
Number of figures: 4
Number of tables: 0
Number of text boxes: 2
Number of references: 33

Statement of authorship: JAO and JFA developed the theory and wrote the first draft of the manuscript. JAO carried out the simulations and produced the figures. JAO analysed the empirical data with support from MCJ. All authors contributed to the ideas and the final manuscript.
Data accessibility statement: Empirical data and code used for simulations are available at `https://github.com/jamesaorr/observation-stressor-interactions`

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Abstract

Understanding the ecological impacts of global change forces us to consider the antagonistic and synergistic interactions between the multiple stressors that ecosystems may face. At the community-level, such interactions are quantified based on the responses of various ecosystem-functioning or diversity metrics. Worryingly, in empirical data, we find that community metrics often observe *opposite* interactions between the same two stressors - sometimes even *systematically*. Here, we investigate this puzzling pattern via a series of geometrical abstractions. By representing stressors and their interactions as displacement vectors in community state-space, and community metrics as directions in this space, we show that the angle between two directions determines the probability, over random stressor combinations, that the metrics will observe opposite interactions. We find that diversity and functioning can easily be associated to opposing directions, which explains the systematic mismatches seen in empirical data.

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1 Introduction

Predicting the combined effects of multiple stressors on ecological communities is a difficult task. The crux of the problem is that stressors often interact in complex ways resulting in unexpected non-additive effects (Côté, Darling, & Brown, 2016; Kroeker, Kordas, & Harley, 2017). Thousands of studies have reported non-additive interactions (antagonistic or synergistic) between specific combinations of stressors on specific biological responses (Jackson, Loewen, Vinebrooke, & Chimimba, 2016; Darling & Côté, 2008; Crain, Kroeker, & Halpern, 2008; Yue et al., 2017), showcasing a huge amount of context-dependency, and highlighting the need, and difficulty, to develop general theory on multiple stressor interactions (Schäfer & Piggott, 2018; De Laender, 2018). Furthermore, although chemists, biologists and ecotoxicologists can sometimes gather detailed knowledge of the mechanisms of stressor interactions at the individual and population levels (Boyd & Brown, 2015; Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007; Rillig, Lehmann, Orr, & Waldman, 2021), research into stressor interactions at the community level is underdeveloped (Orr et al., 2020). Some progress has been made, for example towards understanding the role of species co-tolerance (Vinebrooke et al., 2004; MacLennan & Vinebrooke, 2021) and species interactions (Thompson, MacLennan, & Vinebrooke, 2018; Beauchesne, Cazelles, Archambault, Dee, & Gravel, 2021), but fundamental knowledge gaps remain.

Here we ask a basic, but crucial question: how much does the interaction between stressors depend on the way community-level responses are observed and quantified? To clarify the problem, consider a scenario where an ecologist studies the interactive effects of two stressors on an ecological community (Fig. 1A), using experimental data of the responses to the stressors individually and in combination (Fig. 1B). Suppose they quantify the interaction between those stressors based on the observed responses of species richness and total biomass (Fig. 1C). For species richness they find a synergistic interaction (the combination of stressors caused more extinctions than expected), but for total biomass they find an antagonistic interaction (the combination of stressors caused less change in total biomass than expected). It is concerning that the ecologist's conclusion about whether the stressors interact antagonistically or synergistically depends on how they chose to observe the effects of the stressors on the community.

Different community metrics observing opposite stressor interactions is not a hypothetical problem. In empirical studies of stressor interactions, community metrics often observe qualitatively different stressor interactions (Box 1, Fig. 2). In fact, when function (i.e. biomass) and diversity are both used to quantify stressor interactions, the meta-analysis reported in Box 1 reveals a systematic bias: roughly 75% of observations of interactions are qualitatively different (Box 1, Fig. 2A).

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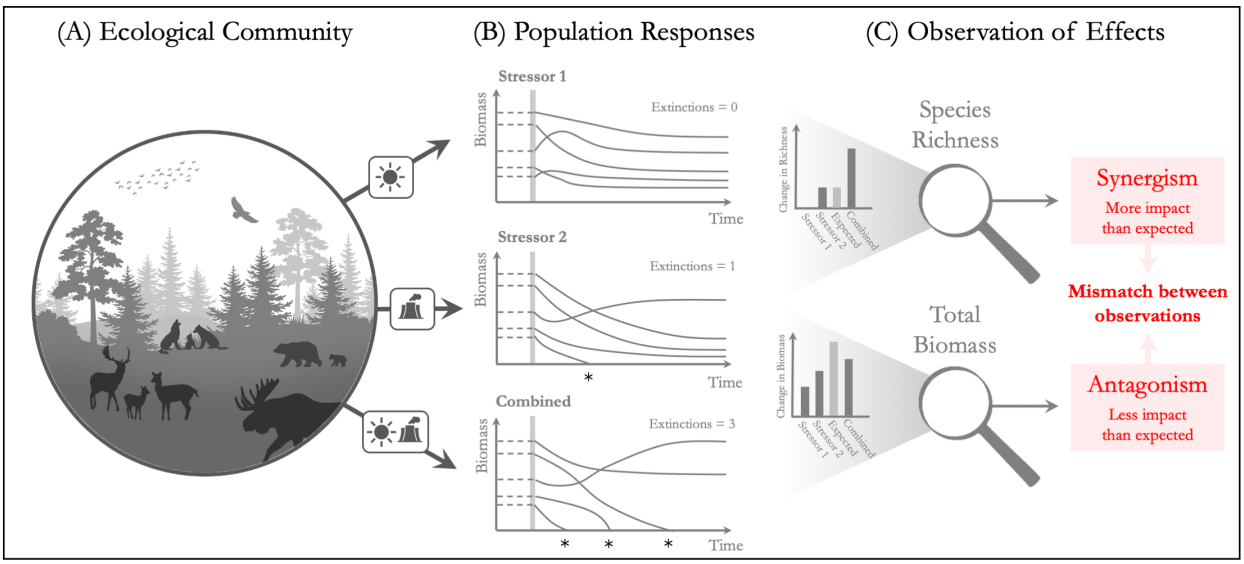

Figure 1: **(A)** An ecological community is impacted by two stressors individually and combined (i.e., a factorial study design). **(B)** Population-level responses are shown by timeseries of biomass where each curve is a single species. The dashed lines represent equilibrium biomasses, the vertical grey bars represent the onset of the (press) stressors and asterisks indicate extinctions. **(C)** The impact of the stressors is observed at the community level using changes in species richness and changes in total biomass. The interaction between the two stressors is quantified using an additive null model (i.e., the combined effect of stressors is predicted to be the sum of the individual effects). Species richness observes a synergistic interaction between the two stressors – there are more extinctions than predicted. Conversely, total biomass observes an antagonistic interaction between the two stressors – there was less change in total biomass than predicted.

Motivated by the concerning empirical patterns reported in Box 1, our goal here is to develop a general theory capable of explaining why community metrics often observe qualitatively different stressor interactions. Our theoretical construction strives to be simple enough to have a chance to be generally applicable to multiple-stressor research, yet complex enough to be informative. Specifically, we convert this ecological problem into a geometric one by representing stressors and their interactions as displacement vectors and community metrics as directions in community state-space. We find that the central ingredient is the co-linearity of observations, which we show can predict the probability of mismatches. Furthermore, we uncover an intriguing link between mismatches at the community level and useful population-level information. Based on our theoretical results we give some recommendations for empiricists interested in multiple-stressor interactions but we also discuss how our approach of comparing observations at the community level to gain insights about the underlying system can be applied more broadly in ecology.

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Box 1: Synthesis of empirical data

To determine how common it is for community metrics to observe opposite stressor interactions, we analysed a database of multiple-stressor experiments in freshwater systems collected for meta-analyses by Jackson et al. (2016) and Morris et al. (2022). 59 of the 125 studies in the database quantified stressor interactions at the community level. There were 16 cases where stressor interactions were reported for both biomass and diversity (Table S1). There were also 12 cases where stressor interactions were reported for both biomass and decomposition (Table S2). Interactive effects between stressors were quantified using Hedges' d (Hedges, 1981). Annotated code for analysis of the empirical data is available in an R notebook at `https://github.com/jamesaorr/observation-stressor-interactions`.

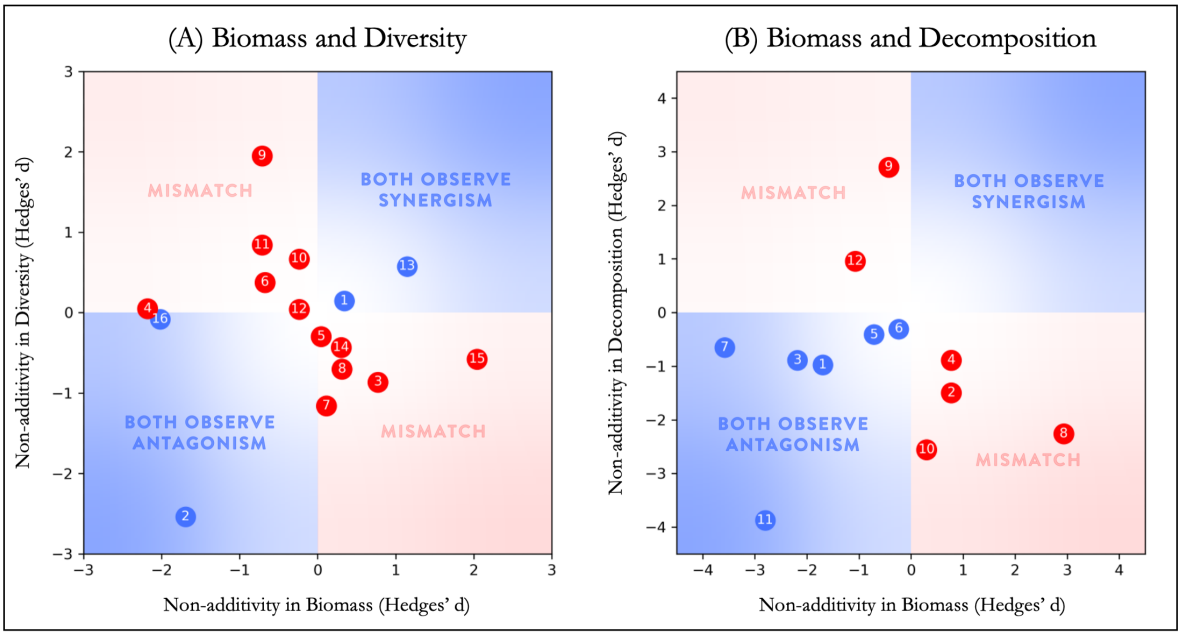

Figure 2. Empirical results where two community metrics were used to observe the interactive effects of the same two stressors on the same community. Both axes show Hedges' d for interactive effects where positive values indicate synergism and negative values indicate antagonism. When points fall in the blue quadrants both community metrics observe the same type of stressor interactions (synergism in the top right and antagonism in the bottom left). However, when points fall in the red quadrants there is a mismatch in the stressor interactions observed. **(A)** Cases where stressors interactions were quantified using a metric describing the biomass of a community and a metric describing the diversity of that same community. **(B)** Cases where stressor interactions were quantified using measures of both biomass and decomposition. See tables S1 and S2 for further details about each data point.

2 Methods

To understand why community metrics often observe opposite stressor interactions, we transform this ecological puzzle into a relatively simple geometric one by making a number of abstractions,

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which are described more formally in Box 2.

First, we consider the effects of stressors on populations as displacement vectors in state-space representations of ecosystems where axes report the species' biomasses (Fig. 3A). Stressor interactions, or non-additivity, can be depicted in these state-spaces by plotting the initial sate of the community, the state of the community following exposure to the stressors individually, the predicted state of the community following exposure to both stressors (based on additivity), and the realised state of the community following exposure to both stressors. The vector of differences between predicted and realised states encodes the non-additivity at the species level, also seen as a displacement vector.

The second level of abstraction is to consider ecosystem functions as positive directions in state-space (Fig. 3B). Total biomass for example is the sum of all the species' biomass and its direction lies exactly between all the axes, giving equal weight to all species. Other functions may not be influenced by the biomass of all species equally. In the hypothetical example shown in Fig. 3B, general decomposition is slightly more sensitive to the biomass of fungi than to the biomass of bacteria, plastic decomposition is primarily carried out by bacteria, and chemical production is primarily carried out by fungi. In general, a positive direction is spanned by a vector of positive values representing the per-capita contribution of each species to the function of interest. The "broadest" function, total biomass, is made up entirely of ones. The "narrowest" functions, are made up entirely of zeroes, expect on the entry associated to the only species contributing to the function (Rivett & Bell, 2018).

Next, we combine these two levels of abstraction to propose a useful representation of the way functions observe non-additivity. To do so, we recenter the state space so that the axes now represent the non-additive effect on each species, with the origin consequently being the predicted state of the community following exposure to both stressors if they did not interact (Fig. 3C). Projecting the non-additivity displacement vector (multi-dimensional) onto the direction of an ecosystem function (one dimension) gives the non-additivity "observed" by that function, which is equivalent to measuring non-additivity as

$$\Delta f(N_{12}) - (\Delta f(N_1) + \Delta f(N_2)) \tag{1}$$

where $\Delta f(N_k)$ refers to the change in a function caused by stressor k. Positive and negative values of non-additivity therefore reflect synergistic and antagonistic interactions respectively.

For each function, drawing a line through the origin and perpendicular to the direction of the function delineates two zones. One where the projection is negative, and thus the function observes an antagonistic interaction (negative non-additivity, less impact than predicted) and the other where the projection is positive and thus the function observes a synergistic interaction (positive non-additivity, more impact than predicted). If the two directions associated to the two functions are not perfectly co-linear, there will be zones of state-space where non-additivity will be qualitatively different when observed by one function or the other. These zones are the two symmetrical cones centered on the origin, formed by the the delineation lines of the functions, perpendicular to their respective directions (red zones in Fig. 3D). The larger the angle between two functions, the larger the zones of mismatches.

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Consequently, if species' non additive responses were random and unbiased, the probability of finding a qualitative mismatch between the two measurement of community-level non-additivity would be:

$$\mathbb{P}(\text{Mismatch}) = \frac{\theta}{\pi} \tag{2}$$

where θ is the angle between the two functions measured in radians. As the exact species contributions to a function may be challenging to acquire in empirical data, it is noteworthy that the angle between two functions can be approximated using only the knowledge, or estimation, of their respective broadness (Eq. (9) in Box 2). Indeed, in a community of S species and functions F_1 and F_2:

$$\cos\theta \approx \cos\theta_{div} = \sqrt{{}^2D\left(F_1\right)/S \ \times \ {}^2D\left(F_2\right)/S} \tag{3}$$

where $1/S \leq \ {}^2D(F)/S \leq 1$ is the broadness of the function F, defined here as the Gini-Simpson diversity index (Hill, 1973) of the vector of species contributions to the function, and normalized by species richness S. Expression (3) quantifies the intuitive expectation that two broad functions ought to be highly colinear, whereas two two narrow functions can be independent (i.e. orthogonal to one another) if they are not performed by the same set of species.

Our final level of abstraction is the realization that measures of diversity, which are highly non-linear functions of species biomass (in the mathematical sense of a function of variables, not in the sense of ecological functioning), can still be placed into this geometric setting by considering their (state-dependent) gradients. The gradient of a diversity metric is a vector encoding its sensitivities to small variations in each species biomass. Importantly, gradients of diversity metrics span non-positive directions in state-space because increasing the biomass of some species (the more abundant ones) decreases diversity.

We carried out basic simulations to compare the observations between and within ecosystem functions of varying broadness and diversity metrics from the family of Hill diversity indices encompassing species richness ($q = 0$), the Shannon index ($q = 1$) and the Gini-Simpson index ($q = 2$) (Roswell, Dushoff, & Winfree, 2021; Hill, 1973). For each pair of community metrics we performed many *in silico* multiple-stressor experiments and recorded the proportion of mismatches of observations of stressor interactions at the community level. Given the generality of our theory, these simulations only need to generate vectors describing non-additivity at the population level, which we can then observed at the community level, and are therefore not required to be highly realistic. We also recorded two pieces of information about the non-additivity at the population level: (i) the consistency of non-additivity (whether or not most species observe antagonistic or synergistic response) and (ii) the scaling of non-additivity by the biomass of species (whether or not more abundant species have larger non-additive responses). Annotated code for our simulations is available in a Jupyter Notebook at `https://github.com/jamesaorr/observation-stressor-interactions`.

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Box 2: Geometrical theory of stressor interactions at the community-level

Here bold symbols denote $S-$dimensional vectors, where S is the richness of the community. Let $\boldsymbol{N}_0$ be the initial state of a community: the vector of species biomass prior to stressor exposure. Let $\boldsymbol{N}_1$ and $\boldsymbol{N}_2$ be the community states after exposure to stressor 1 and 2, respectively. Let $\boldsymbol{N}_{12}$ be the state following exposure to both stressors. The observed-non additive response, quantified via an ecosystem function $f(\boldsymbol{N})$, is

$$\Delta f = f(\boldsymbol{N}_1) + f(\boldsymbol{N}_2) - f(\boldsymbol{N}_{12}) - f(\boldsymbol{N}_0). \tag{4}$$

The interaction type –antagonistic or synergistic– is determined by the sign of Δf. If positive, more change occurred than expected, thus a synergistic interaction. If negative, less change occurred, thus an antagonistic interaction took place between the two stressors. For a linear function there exist a constant c (that will play no role in what follows) and a vector $\boldsymbol{\varphi}$ –the gradient– such that

$$f(\boldsymbol{N}) = c + \langle \boldsymbol{\varphi}, \boldsymbol{N} \rangle \tag{5}$$

with $\langle \cdot, \cdot \rangle$ the scalar product of vectors. The elements of the gradient vector $\boldsymbol{\varphi}$ encode the per capita contribution of species to the function. For us it will not matter what those exact contributions are, only relative species contributions which determine the *direction* spanned by the vector $\boldsymbol{\varphi}$. A positive function is such that the elements of the gradient are positive. If we rewrite the non additive response of the function, we get that

$$\Delta f = \langle \boldsymbol{\varphi}, \Delta \boldsymbol{N} \rangle \tag{6}$$

where $\Delta \boldsymbol{N} = \boldsymbol{N}_1 + \boldsymbol{N}_2 - \boldsymbol{N}_{12} - \boldsymbol{N}_0$ is the vector of species-level non additivity. For non-linear functions the (state dependent) gradient vector can be computed as $\varphi_i(\boldsymbol{N}_0) = \frac{\partial f}{\partial N_i}|_{\boldsymbol{N}_0}$. In this case, expression (6) will be an approximation, exact only for weak stressors. Now, for two functions, f , g associated to two directions spanned by the two gradient vectors $\boldsymbol{\varphi}$ and $\boldsymbol{\phi}$, we define their colinearity as the angle $0 \leq \theta < 2\pi$ whose cosine is

$$\cos\theta = \frac{\langle \boldsymbol{\varphi}, \boldsymbol{\phi} \rangle}{\|\boldsymbol{\varphi}\| \, \|\boldsymbol{\phi}\|} \tag{7}$$

where $\|\cdot\|$ denotes the Euclidian norm of vectors. A graphical argument (Fig. 3D) tells us that the fraction of non-additive vectors $\Delta \boldsymbol{N}$ that will lead to a qualitative interaction mismatch between the observations of f and g is

$$\mathbb{P}(\text{sign}(\Delta f) \neq \text{sign}(\Delta g)) = \frac{\theta}{\pi} \tag{8}$$

In such cases, one of the functions will observe a synergistic interaction between stressors, while the other function will observe an antagonistic interaction. For random positive directions, we can evaluate the cosine of the angle based on a notion of functional broadness. Indeed, given a random choice of positive functions

$$\frac{\langle \boldsymbol{\varphi}, \boldsymbol{\phi} \rangle}{\|\boldsymbol{\varphi}\| \, \|\boldsymbol{\phi}\|} \approx \frac{1}{S} \frac{\sum \varphi_i \sum \phi_i}{\sqrt{\sum \varphi_i^2 \sum \phi_i^2}} = \frac{1}{S} \sqrt{\frac{1}{\sum (\frac{\varphi_i}{\sum \varphi_i})^2} \frac{1}{\sum (\frac{\phi_i}{\sum \phi_i})^2}} = \sqrt{\frac{{}^2D_f}{S} \frac{{}^2D_g}{S}} \tag{9}$$

where ${}^qD$ denotes Hill's diversity index. We will call the fraction $\frac{{}^2D_f}{S}$ the *broadness* of the function f, which is maximal (and equal to one) if all species contribute equally to the function (i.e. total biomass).

We can modify the above theory to account for an additional piece of species-level information in the form of a biomass scaling of species-level non-additivity. It is indeed reasonable that more abundant species will, in absolute terms, show a larger response to stressor exposure. For some scaling exponent $\alpha \geq 0$, if we denote D the diagonal matrix whose elements are the species biomass prior to stressor exposure, we may assume that the non additive displacement vector takes the form $\Delta \boldsymbol{N} = D^\alpha \boldsymbol{\Delta}$. We then have that

$$\Delta f = \langle D^\alpha \boldsymbol{\varphi}, \boldsymbol{\Delta} \rangle \tag{10}$$

the relevant angle to consider then becomes

$$\cos\theta_\alpha = \frac{\langle \boldsymbol{\varphi}, D^{2\alpha} \boldsymbol{\phi} \rangle}{\|D^\alpha \boldsymbol{\varphi}\| \, \|D^\alpha \boldsymbol{\phi}\|} \tag{11}$$

giving the fraction of rescaled vectors $\boldsymbol{\Delta}$ that would lead to a qualitative mismatch.

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3 Results

3.1 Mismatches between functions

As predicted by our geometrical arguments, in simulations, the proportion (over random *in silico* experiments) of mismatches between the observations of two ecosystem functions closely reflects their co-linearity, as defined by the angle between their respective directions (Eq. 2, Fig. 3E). We also confirm that this angle can be estimated using only the functions' respective broadness (Eq. 3, Fig. 3E inset). However, we see that the probability of mismatches is accurately predicted only when non-additivity is unbiased at the population level; that is when approximately half the species show synergistic responses and half antagonistic ones. On the other hand, if population-level non-additivity is biased towards antagonism or synergism, the prediction based on the angle between functions will overestimate the proportion of mismatches (Fig. 3E). This could be seen as a limitation, but it actually provides a useful link between mismatches in observations at the community level and information on population-level responses. This effect occurs because when non-additivity vectors are mostly synergistic or antagonistic, they tend to fall in the areas where positive linear functions must always observe the same non-additivity (top right and bottom left quadrants in Fig. 3D). The empirical data showing a 50% rate of mismatches between total biomass and decomposition (Box 1, Fig. 2B) suggests that decomposition is typically a more narrow function than total biomass, sensitive to the biomass of a subset of the community, and that the non-additive effect of stressors at the species-level (in the ecosystem context) is largely inconsistent, with species as likely to perceive synergistic or antagonistic interactions between stressors.

3.2 Mismatches between diversity metrics

From the angle between the gradients of diversity metrics, we can still predict the probability of mismatches. Here we are comparing metrics from the family of Hill diversity, which unifies the classic notions of diversity that ecologists use (richness, Shannon index, Simpson index) into one general framework where metrics vary based on q, the hill exponent, which controls their sensitivity to common or rare species (Roswell et al., 2021). Consequently, we see that the difference in the q values between two diversity metrics correlates to the size of the angle between their gradients (Fig. 4A). Here, the consistency of population-level non-additivity has a weak effect due to the non-linearity of diversity metrics. In fact, this non-linearity of diversity metrics is capable of introducing non-additivity between stressors even if there is no non-additivity at the population-level (Fig. 4B). Furthermore, the evenness of the biomass distribution of a community determines how similar gradients of diversity metrics are to positive functions. For uneven communities, increasing the biomass of most species will increase diversity so gradients will behave similarly to positive linear functions. However, for perfectly even communities, increasing the biomass of any single species will decrease diversity so gradients of diversity will effectively be negative functions of biomass.

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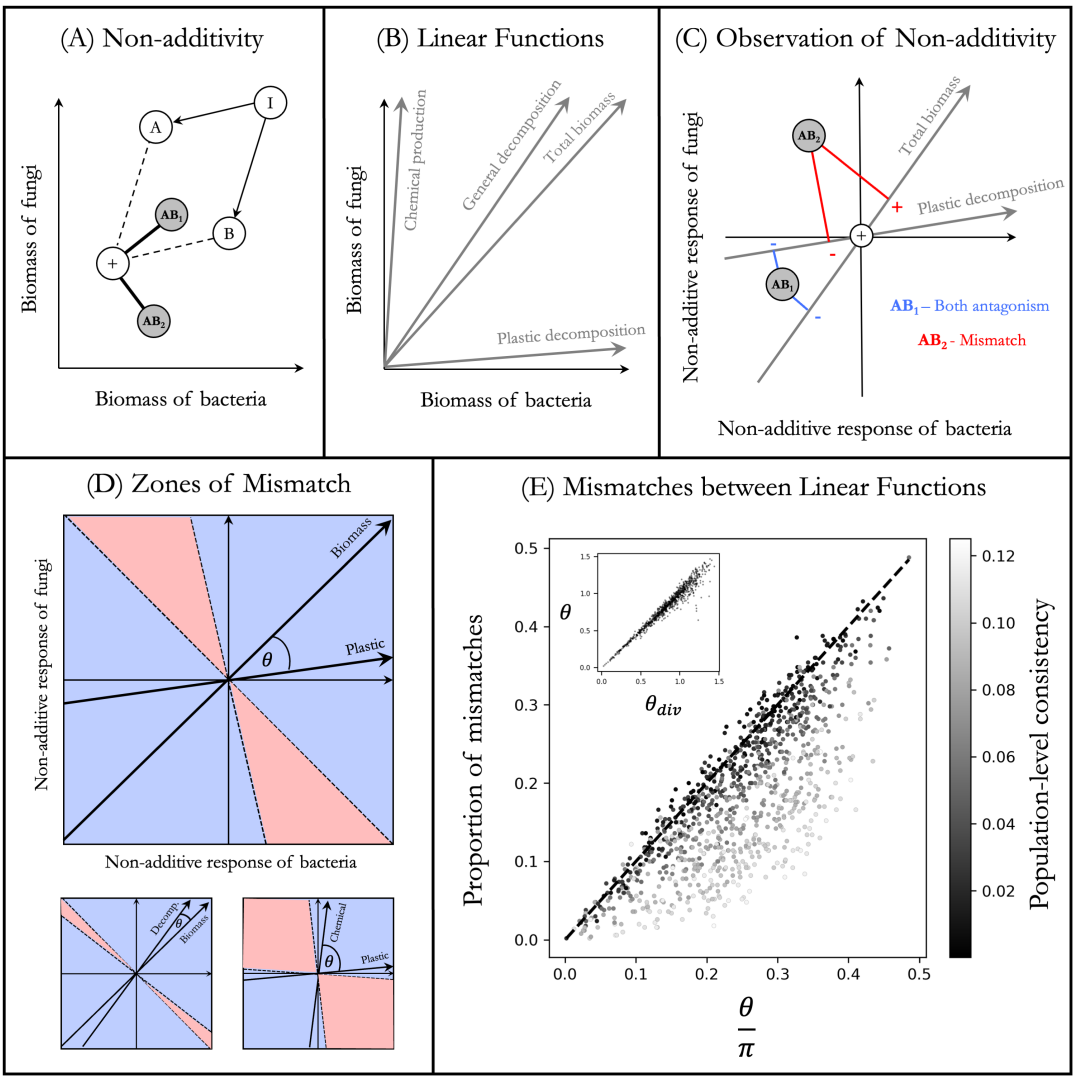

Figure 3: **(A)** Stressors and their non-additive interactions can be viewed as displacement vectors in community state-space. Here a community of bacteria and fungi is impacted by two stressors, represented by the black arrows from the initial state of the community (I) to the points A and B. The predicted state following exposure to both stressors (+) is based on an additive null model. The points AB_1 and AB_2 are two examples of realised states following exposure to both stressors. The thick black lines between the predicted and realised states therefore represent examples of non-additive effects. **(B)** Measures of ecosystem function can be represented as positive directions in this state-space. **(C)** Realised states are plotted in state space where the additive expectation is at origin and each axis describes the non-additive effect on each species. Here the non-additive vectors associated with the realised states AB_1 and AB_2 from (A) are projected onto total biomass and plastic decomposition. For AB_1, both community metrics observe antagonism. However, for AB_2 there is a mismatch in the observations of non-additivity: total biomass observes synergism while plastic decomposition observes antagonism. **(D)** For two functions, the zones of mismatches in their observations can be found by drawing lines perpendicular to the functions that go through the origin. Community metrics will observe different stressor interactions for non-additive vectors that fall between these lines (i.e., in the red zones). **(E)** Over many simulated multiple-stressor experiments, the proportion of mismatches between linear functions can be predicted by the angle between them in radians (θ) divided by the number π. When non-additivity is consistent at the species-level there are less mismatches than predicted as non-additivity vectors tend to fall in the mostly positive or mostly negative areas of state-space, which happen to overlap with the zones of consistent observations for linear functions (i.e., blue zones in (D)). The inset shows how the angle between two functions can be predicted using their diversities.

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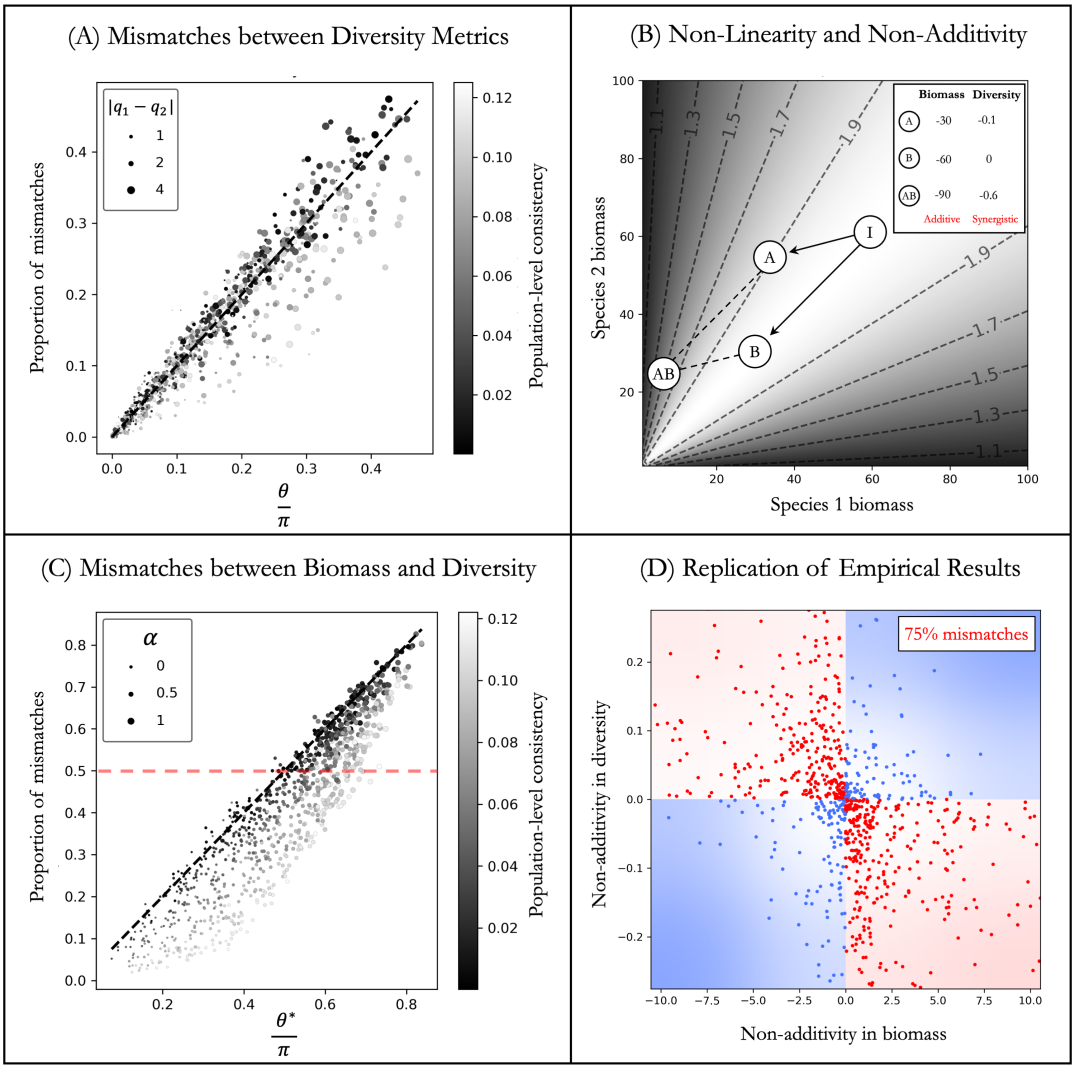

Figure 4: **(A)** The proportion of mismatches between two diversity metrics is predicted by the angle between their gradient vectors. Increasing the difference between the q values of diversity indices increases the angle between their gradients, therefore increasing the proportion of mismatches. **(B)** Heat map with contour lines depicting the Simpson's Diversity of a two-species community overlain on community state-space where each axis depicts the biomass of a single species. Other measure of diversity (e.g., Shannon index) have different spacing between their contour lines. Here the two species are being impacted by two stressors, represented by the black arrows from the initial state of the community (I) to the points A and B. There is no non-additivity at the population level (the point AB is exactly where an additive null model would have predicted). Linear functions (e.g. total biomass) will therefore observe no non-additivity. However, the non-linearity of functions such as diversity can introduce non-additivity at the community level as is the case in this example. **(C)** The angle between the direction of total biomass and the gradient of a diversity index (here $q = 2$) predicts the proportion of mismatches between these two very different community metrics. Specifically, the relevant angle is between total biomass and the gradient of diversity after they have also been scaled by the biomass of each species (θ^*). When non-additivity is scaled by species biomass ($\alpha > 0$) total biomass and diversity can effectively become opposite functions. Points above the dashed red line show cases where there is a systematic mismatch in the observations of total biomass and diversity. **(D)** The empirical results from Fig. 2A can be recreated by simulating multiple-stressor experiments where population-level non-additivity is relative to species' biomass.

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3.3 Mismatches between function and diversity

Bringing these groups of community metrics together, the angle between a positive function and the gradient of a diversity metric can be used to predict the probability of mismatches in their observations (Fig. 4C)). Like before, consistency of non-additivity at the population level causes the prediction to overestimate the actual proportion of mismatches. However, we now see that the angle between these two community metrics can exceed 90 degrees leading to a systematic bias towards mismatches of observations. This intriguing result is connected to a second piece of population-level information: the scaling of non-additivity by species biomass (Eq. (11) in Box 2).

When non-additive effects are significantly larger for more abundant species ($\alpha > 0.5$), function and diversity are expected to observe opposite stressor interactions (larger points are above the red line in Fig. 4C). If non-additivity causes the biomass of abundant species to decrease, total biomass will decrease but diversity will increase. If on the other hand, non-additivity causes the biomass of abundant species to increase, total biomass will increase but diversity will decrease. It is important to note, that when non-additivity is scaled by biomass, the relevant angle, θ^*, is between the function and the gradient of diversity after they have been scaled in the same way by biomass. The empirical data (Box 1, Fig. 2A), can be easily replicated by simulating many multiple-stressor experiments and comparing how function and diversity observe stressor interactions. To recreate the empirical results (i.e., 75% mismatches), the only requirement is that non-additivity must be scaled by biomass (Fig. 4D).

4 Discussion

Our geometric approach has shed some light on multi-stressor interactions at the community level. Qualitative mismatches between the observations of community metrics should no longer be surprising, even metrics describing the same aspect of a community (i.e., either its functioning or diversity) can easily observe opposite interactions between the same two stressors. With our theory, mismatches between observations at the community level are predictable, and can even reveal useful information about lower-levels of biological organization. Mismatches between measures of functioning indicate their broadness (i.e., how many species contribute to the functions) while mismatches between diversity metrics indicate their sensitivity to rare or common species (i.e., hill exponent).

Ecological research is typically reductionist, using information about individuals and populations to understand communities and ecosystems (Loreau, 2010). Our work demonstrates the reverse approach by using information about communities to understand population-level responses. Firstly, we found that when species' responses are consistently antagonistic or synergistic the co-linearity of community-level observations will overestimate the probability of mismatches. This consistency of population-level non-additivity will be determined by the sources of non-additivity. If non-additivity is generated between the stressors themselves (Boyd & Brown, 2015; Rillig et al., 2021) – perhaps via strong chemical or physical interactions (e.g., two benign chemicals could become very toxic when

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combined) – then all species may observe the same interaction and the probability of mismatches, even between very different community metrics, could be low. On the other hand, if non-additivity is coming from a range of sources (e.g., species interactions, invasions, extinctions) then population-level responses may be inconsistent and the co-linearity of observations will predict the probability of mismatches. Secondly, comparing observations of function and diversity can reveal whether or not there is some biomass scaling of population-level non-additivity. Indeed, if stressors (and their interactions) impact species in similar ways, it is expected that more abundant species would show larger responses in absolute terms (Arnoldi, Loreau, & Haegeman, 2019; Supp & Ernest, 2014). It is this scaling by biomass that allows function and diversity to systematically observe opposite stressor interactions. For instance, non-additivity that increases the biomass of abundant species will increase total biomass but decrease diversity. As such, the meta-analysis in Box 1 opens a window through which we can study population-level non-additivity from the top down.

Our research focused on multiple-stressor interactions as their direction (antagonism versus synergism) carries so much weight for researchers in that field; there is evidence of a publication bias towards synergism (Côté et al., 2016) and vote-counting of interaction types is a common, but flawed, approach for generalisation (Griffen, Belgrad, Cannizzo, Knotts, & Hancock, 2016). More broadly, the link between mismatches at the community level and population-level information is not specific to stressor interactions. Our geometric approach could have focused on single stressors rather than on the non-additive effects of multiple stressors. Mismatches between community-level observations of a single stressor would reveal the consistency of species' responses to that stressor (i.e., response diversity *sensu* Elmqvist et al. (2003)), and the relationship between species' responses and their biomass (i.e., perturbation type *sensu* Arnoldi et al. (2019)). Perhaps multi-functional approaches can be leveraged to gain insights into population-level dynamics from the top down, and in an ecosystem context, by contrast to controlled experiments where populations or even organisms are studied in isolation (Bergelson, Kreitman, Petrov, Sanchez, & Tikhonov, 2021). It is well appreciated in ecology that by reducing the complexity of an ecosystem down to a single number, community metrics can hide important information about the underlying system (Hurlbert, 1971; Tilman, 1996). We have found, however, that comparing the observations of multiple community metrics gives us an opportunity to regain some useful information about population-level dynamics.

4.1 Recommendations for empiricists

Returning to the highly applied field of multiple-stressor research, we have some recommendations for empiricists arising from our theory that we hope will reduce context-dependency in the field and may help to uncover generalities.

(i) Recognise that stressor interactions at the community level heavily depend on the way we observe the system. Since two community metrics can observe opposite interactions between the same stressors, it is unwise to think of stressor interactions at the community level as "intrinsic" to the stressors themselves. As there is growing interest in the existence of context

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dependency of stressor interactions (Turschwell et al., 2022; King et al., 2022), development of general theory is sorely needed. Our work offers a mechanistic explanation for one of the drivers of this context dependency: observations at the community level. More broadly, our work illustrates a common form of context-dependence in ecology that is caused by methodological differences between studies (Catford, Wilson, Pyšek, Hulme, & Duncan, 2021).

(ii) Do not aggregate community metrics in meta-analyses. It is common practice for meta-analyses to aggregate the observations of different community metrics to make generalisations about multiple-stressor interactions at the community level (Jackson et al., 2016; Crain et al., 2008; Morris et al., 2022). In light of our theory, this approach does not provide useful insights. Even combining different measures of function (e.g., total biomass and decomposition) or of diversity (e.g., richness, evenness) is not a sensible approach. Moving forward, meta-analyses should only aggregate results obtained using the exact same community metric to make generalisations about combinations of stressors or study systems.

(iii) Be careful interpreting stressor interactions observed by diversity metrics. As mentioned before, diversity metrics are highly non-linear functions of species biomass. Consequently, linear responses of species' biomass can easily be observed as non-linear responses of diversity. The non-linearity of diversity metrics can of course translate into non-additivity between stressors even if there are no direct interactions between the stressor and there are no biological sources of non-additivity (Fig. 4B). It therefore does not make sense to use an additive null model to predict multiple-stressor impacts on diversity. Furthermore, non-linear aggregate properties, such as diversity, are sensitive to dimensional effects when scaling up predictions from the species level to the community level (Orr, Piggott, Jackson, & Arnoldi, 2021).

(iv) Measure and report stressor interactions at the community level using multiple observations. When studying multiple-stressor impacts at the community level, we suggest measuring and reporting multiple complementary observations describing both the diversity and functioning of the community. It is only by comparing multiple observations that we can study the biological mechanisms of stressor interactions at the community level. The interactions observed by each observation, and the probability of their mismatches (revealing the consistency and biomass scaling of population-level non-additivity), will give insights into potential mechanisms of non-additivity such as species interactions, extinctions and invasions.

4.2 Conclusions

Our work offers a platform from which to study stressor interactions at the community-level, explaining why qualitative mismatches are to be expected, but also revealing what can be learned from those mismatches about underlying population-level processes. Given the overwhelming context-dependency of multiple-stressor research, basic theoretical developments, such as our geometric approach, have potential to add clarity and direction to the field. The fact that our very simple theory could provide

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useful insights demonstrates that there is still much to learn about stressor interactions at the community level. Building on our work, a promising approach would be to use the rich theoretical frameworks developed in community ecology to build general expectations for the ecological impacts of multiple stressors.

Acknowledgements

JAO and MCJ were supported by a Natural Environment Research Council grant (NE/V001396/1). JAO was supported by an Irish Research Council Laureate Award (IRCLA/2017/112) and TCD Provost's PhD Award held by JJP. JFA and ALJ were supported by an Irish Research Council Laureate Award (IRCLA/2017/186). JFA was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41).

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