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Uncovering the mechanisms underpinning divergent environmental change impacts on biodiversity and ecosystem functioning

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Abstract

Environmental change drivers (ECDs) impact ecological communities in various ways, from enrichment that increases species' performance and abundance, to stressors that reduce their reproduction and growth. These effects can affect species coexistence as well as impact ecosystem functioning and the relationship between biodiversity and ecosystem function (BEF). Predicting the impact of ECDs on communities and BEF relationships requires understanding how ECDs affect fundamental population parameters, including intrinsic rate of increase (r), carrying capacity (K), and interspecific interactions (α). Here, we use numerical simulations based on theoretical models to show the explicit links between these parameters and the nature of BEF relationships. Depending on the mean and variance of the effects of ECDs on community members, BEF relationships increase or decrease in both their intercept and slope. We further derive hypotheses about how BEF relationships will be affected by multiple ECDs or when we consider multiple ecosystem functions. Our simple approach to understanding how ECDs affect BEF relationships provides a robust framework to explain why disparate studies and meta-analyses come to opposing conclusions about resilience or sensitivity of BEF relationships to anthropogenic influences. We show that modeling approaches offer a generalized and predictive understanding to guide biodiversity conservation, restoration, and green infrastructure design under environmental change.

KEYWORDS

coexistence, disturbance, ecological communities, global change, Lotka–Volterra model, multiple stressors, pollution, population parameters, species interactions

INTRODUCTION

Anthropogenic drivers of environmental change are globally ubiquitous and, in some regions, more important than natural mechanisms that historically structure patterns of biodiversity (Helmus et al., 2014; Lu et al., 2020). There is now ample evidence, especially from aquatic systems, that these drivers and stressors alter biodiversity patterns individually and in combination (e.g., O'Brien et al., 2019; Townsend et al., 2008). Additionally, there is widespread concern about how the effects of these drivers scale up to impacts on ecosystem functioning and their ability to deliver benefits to human populations

(Bell et al., 2017; Cardinale et al., 2012; Jackson et al., 2016; Sandifer et al., 2015).

Environmental or global change drivers and stressors are broad terms that capture a diversity of effects. From here on, we refer to them as environmental change drivers (ECDs), since we do not consider drivers that operate at particular scales, but rather drivers that can manifest impacts at community scales, from a local release of a pollutant to global climate change. ECDs are any external factor that deviates from historical norms due to anthropogenic activities and that has demonstrable effects on individuals, populations, communities, or ecosystems. These effects can be positive or negative (Jackson et al., 2016) and even negligible at one scale or point in time but result in larger scale or longer-term effects (Rohr et al., 2013). We refer to positive effects of ECDs as enrichment, nonlethal negative effects as stressors (e.g., reduced growth, failed reproduction, and suboptimal foraging), and lethal events that reduce abundance and/or diversity as disturbances. Larger scale or longer-term consequences of these effects that result in reduced diversity, resilience, and functions and services are referred to as degradation.

There is a widely understood relationship between biodiversity and the functioning and service delivery of ecological communities and ecosystems (here we refer to this relationship generally as the biodiversity-ecosystem function relationship, BEF; Gamfeldt et al., 2013; Hooper et al., 2005; Tilman et al., 2014). Several mechanisms have been proposed to explain the BEF relationships and their dependence on scale (Gonzalez et al., 2020) or trophic level of the organisms considered (Raffaelli, 2006; Xiao et al., 2018). For our purposes, we will assume that within-trophic level BEF relationships and species contributions to BEF result either from competitive dominance (selection effect) or some form of complementary contribution (Loreau & Hector, 2001). This complementarity can emerge through various mechanisms, such as niche partitioning, dilution effects on pathogens, facilitation, and so on, and ECDs are likely to affect multiple mechanistic pathways that determine how biodiversity influences ecosystem function (De Laender et al., 2016). Although there are multiple types of ecosystem functions that are dependent on direct species contributions to function (Cadotte et al., 2017) or their effect traits (Chapin, 2003; Lavorel & Garnier, 2002), we largely focus on community biomass, which is directly influenced by coexistence and is often correlated with total abundance. We will touch on other types of contributions to function toward the end of this article.

At a minimum, any ECD that causes a loss in biodiversity should also result in a decline in ecosystem functioning. However, this expectation is only valid when the ECD causes the removal of species from a regional species pool and they are no longer able to colonize a local community, thus reducing maximum local diversity (Hagan et al., 2021). Of course, there are specific circumstances that might differ from this scenario at the local scale (Dee et al., 2023), for example, if a rare allelopathic plant is extirpated, with the result being a potential increase in local function. In reality, most ECDs have more complicated effects than just species removal and are likely to alter BEF relationships even if no species are lost (Du et al., 2024; Mensens et al., 2015; Spaak et al., 2017). This can happen if ECDs alter some combination of intrinsic rate of increase, carrying capacity, or the strength of interspecific interactions, all of which will have implications for selection and complementarity effects (De Laender, 2018; De Laender et al., 2016; Li et al., 2010; Van Moorsel et al., 2022).

A recent meta-analysis (Hong et al., 2022) assessed whether ECDs alter BEF relationships by synthesizing experimental evidence. They concluded that "...biodiversity effects on ecosystem functioning were larger in stressful environments... indicating that high-diversity communities were more resistant to environmental change." This seemingly indicates that higher biodiversity is resilient against the effects of ECDs and that we might not expect that ECDs cause decreases in function. Certainly, enriching ECDs will cause increases in function (Reich et al., 2001). However, other studies indicate that ECDs do, in fact, cause declines in both biodiversity and ecosystem function (BEF), from local to global scales (Rillig et al., 2019, 2023; Sánchez-Bayo & Wyckhuys, 2019). Studies of ECDs on biodiversity or function frequently evaluate very different ECDs—including changes in natural environment gradients like CO_2 enrichment, warming, nutrient addition, and drought (e.g., Hong et al., 2022) and more anthropogenic factors like heavy metal contamination, increased salinity, changes in pH (e.g., Rillig et al., 2023).

The reality is that the response of communities and their functioning to ECDs is complex because ECDs variously include enrichment and stressors (De Laender et al., 2016; Dieleman et al., 2015). We argue that the divergent inferences from experiments and meta-analyses evaluating ECD effects on diversity and function are generally explained by the combination of the magnitude of the ECD effect and its variance of effect on fundamental parameters across species in an assemblage. We build on the reasoning from previous studies (e.g., De Laender, 2018; De Laender et al., 2016; Van Moorsel et al., 2022) arguing that ECDs that affect fundamental population parameters can influence ecosystem functioning in predictable ways.

Species coexistence is a fundamental component that underpins BEF mechanisms (Carroll et al., 2011; Loreau et al., 2012; Steudel et al., 2011; Turnbull et al., 2013). Key to coexistence are population parameters such as

intrinsic rate of increase, carrying capacity, and competitive interactions (Chesson, 2000). While there has been some debate about how coexistence components impact complementarity and selection effects (e.g., Carroll et al., 2011; Loreau et al., 2012), we simply assume that BEF relationships are enhanced by coexistence mechanisms, namely that stabilizing coexistence mechanisms result in greater abundance and higher function than a community determined by neutral processes (Turnbull et al., 2016). Changes in environmental conditions can enhance or reduce coexistence depending on individual species responses to changing conditions and whether these reinforce fitness differences that result in competitive exclusion or strengthen trade-offs that allow coexistence (Chesson & Huntly, 1997; Descamps-Julien & Gonzalez, 2005; Firkowski et al., 2022). For our purposes, we consider ECD effects on three fundamental population parameters: (1) carrying capacity, (2) strength of competition/niche differences, and (3) intrinsic rate of increase. Using numerical simulations, we examine how changes in the mean magnitude and variance among species of these key parameters can affect the relationship between BEF. Our simulations rely on a combination of simple Lotka–Volterra models and a derivation of Chesson's coexistence theory (Adler et al., 2010; Chesson, 2000) to assess how changes in parameters impact ecosystem functioning (Box 1). For our simulations, we measure ecosystem function as the sum of biomass in an assemblage. While many functions can be measured from real assemblages (Cadotte et al., 2017; Hector & Bagchi, 2007; Zavaleta et al., 2010), most experiments measure biomass production as the only or primary measure of ecosystem function (Tilman et al., 2014).

Our conceptual treatment of the effects of ECDs on BEF relationships is intended to shed light on small-scale experiments that manipulate species diversity and ECDs, and not an analysis to provide a more general understanding of how complex natural ecosystems should respond to ECDs. We argue that our approach is necessary because BEF-ECD experiments have been and are being performed without the correct conceptual and theoretical underpinning to evaluate the potential effects of ECDs. Further, our framework presented in this paper explains why there might be inconsistencies among experiments.

CONSEQUENCES OF ENVIRONMENTAL CHANGE ON COEXISTENCE AND ECOSYSTEM FUNCTIONING

ECDs have consequences for coexistence and species contributions to function by impacting basic population-level processes. Here, using a two-species Lotka–Volterra model, we first explore how ECD-induced changes in population-level parameters affect species coexistence and ecosystem functioning.

ECD changes mean carrying capacity (K)

ECDs that enrich local carrying capacities K, by, for example, adding a limiting nutrient or extending the growing season, without altering other population dynamics, can increase total community abundance, resulting in higher function if all species are affected by the ECD similarly. Obviously, the converse is true; an ECD that acts as a stressor that reduces K will decrease overall function.

ECD increases the variation in carrying capacity (K)

Unequal responses among species in their K to ECDs are expected if the drivers act on existing trade-offs, say on soil moisture. If changes to K among species are symmetric—an increase in one species is matched by a decrease in another—then there will be little effect on the community function as a result of density compensation (Macarthur et al., 1972) or compensatory dynamics (Gonzalez & Loreau, 2009). This is because the predicted mean of the two monocultures should remain unchanged, and the total community function also remains unchanged. However, selection effects should increase with an increase in the difference in K because some species will see an increase in their contribution to the function of the community.

Asymmetric ECD effects on K will impact fitness differences among species (Box 1, Figure 1). ECDs can serve as an equalizing mechanism by reducing fitness differences (Chesson & Huntly, 1997) that, for example, shift species from a region of competitive exclusion to coexistence (Figure 1). On the contrary, ECDs can enhance existing trade-offs or create fitness inequalities because species have differing sensitivities to ECD effects (Figure 1).

The effects of asymmetric ECD on K can also affect niche differences due to how niche differences are calculated (Box 1). Therefore, changes in K can increase or decrease niche overlap, as can be seen by the angle of the vectors in Figure 1, vectors **A** and **B**. Vector **A** shows how a decline in K for the higher fitness species increases the probability of coexistence, while vector **B** shows the outcome of increasing fitness differences. In summary, ECDs can have a diversity of impacts on community

BOX 1 Modeling species dynamics and coexistence

Fundamental properties of population dynamics and coexistence have been described in long-established mathematical models, which we employ to showcase how key parameters alter simple two-species assemblages. We utilize classic Lotka–Volterra competition models and modern coexistence theory (Chesson, 2000) to illustrate how changes to parameters influence community biomass.

We start with two coupled Lotka–Volterra competition models:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right) \text{ and } \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}\right), \quad (1)$$

where N_1 and N_2 are the population sizes of species 1 and 2, respectively, r and K are the intrinsic rate of increase and carrying capacity, and α_{12} and α_{21} are the coefficients of competition for the effect of species 2 on species 1 and vice versa, respectively. We simulate population change using these coupled models in discrete time steps to assess the effect of ECDs on these parameters.

An alternative expression of the Lotka–Volterra model (e.g., Adler et al., 2007, 2010; HilleRisLambers et al., 2012), which explicitly includes intraspecific competition strength α'_{11} and α'_{22}, referred to as absolute intraspecific competition coefficients (Chesson, 2000), reads as follows:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(1 - \alpha'_{11} N_1 - \alpha'_{12} N_2\right) \text{ and } \frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left(1 - \alpha'_{22} N_2 - \alpha'_{21} N_1\right). \quad (2)$$

From this expression, niche overlap (ρ) and fitness difference (κ_1/κ_2) are given by Chesson and Kuang (2008):

$$\rho = \sqrt{\frac{\alpha'_{12}\alpha'_{21}}{\alpha'_{11}\alpha'_{22}}} \text{ and } \frac{\kappa_1}{\kappa_2} = \sqrt{\frac{\alpha'_{21}\alpha'_{22}}{\alpha'_{21}\alpha'_{11}}}. \quad (3 \text{ and } 4)$$

The condition for coexistence is given by

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho}. \quad (5)$$

From the two expression Equations (1) and (2), we know that

$$\alpha'_{11} = \frac{1}{K_1}, \quad \alpha'_{22} = \frac{1}{K_2}, \quad \alpha'_{12} = \frac{\alpha_{12}}{K_1}, \quad \alpha'_{21} = \frac{\alpha_{21}}{K_2}. \quad (6)$$

Combining Equations (3), (4), and (6) leads to ρ and κ_1/κ_2 under the first expression Equation (1):

$$\rho = \sqrt{\alpha_{12}\alpha_{21}} \text{ and } \frac{\kappa_1}{\kappa_2} = \frac{K_1}{K_2}\sqrt{\frac{\alpha_{21}}{\alpha_{12}}}, \quad (7 \text{ and } 8)$$

which makes clear that the niche overlap is determined solely by per capita interspecific competition coefficients α_{12} and α_{21}, while fitness difference is determined jointly by competition coefficients α_{12} and α_{21} and carrying capacity K_1 and K_2. From this, niche difference is simply $1 - \rho$.

Here, then, ECDs influence niche overlap by changing interspecific competition, whereas changes to fitness differences can be impacted by ECDs in more complex ways, acting on either or both of carrying capacity and competition coefficients.

Finally, ecosystem function is calculated as the total community abundance, the most commonly calculated measure of function (Tilman et al., 2014). Other modeling analyses that evaluate diversity effects on function similarly sum abundances (Firkowski et al., 2022; Thompson et al., 2020).

biomass depending on the magnitude and variation of the effects of ECDs on *K*. In multispecies systems, moving from coexistence to exclusion could simply reduce function by decreasing richness along the existing BEF relationship, but affecting the magnitude of fitness or niche differences should impact BEF slopes and intercepts regardless of whether species are extirpated (see *Environmental change impacts on BEF relationships under realistic scenarios*).

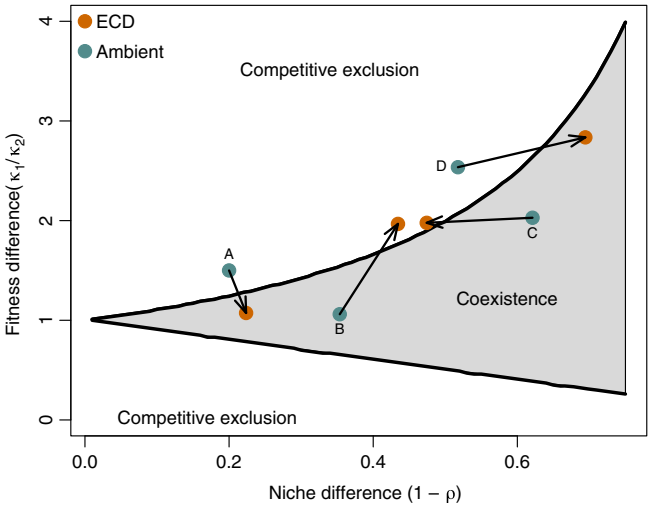

FIGURE 1 Chesson's coexistence framework showing how changes in carrying capacity (*K*) or per capita competitive strengths (α) can change the coexistence/exclusion outcomes. The equations used to generate the curves are shown in Box 1. Vectors **A** and **B** are the outcomes of changes in *K* of one species, and **C** and **D** represent changes in α's. The parameter values for **A** go from (turquoise dot) $K_1 = 15$, $K_2 = 10$, $\alpha_{12} = 3$, $\alpha_{21} = 2$, to (orange dot) $K_1 = 12$. For **B**, from $K_1 = 12$, $K_2 = 8$, $\alpha_{12} = 6$, $\alpha_{21} = 2$, to $K_2 = 5$. For **C**, from $K_1 = 14$, $K_2 = 10$, $\alpha_{12} = 6$, $\alpha_{21} = 9$, to $\alpha_{12} = 4.7$ and $\alpha_{21} = 6.7$. For **D**, from $K_1 = 14$, $K_2 = 8$, $\alpha_{12} = 5$, $\alpha_{21} = 9$, to $\alpha_{12} = 6$ and $\alpha_{21} = 9$.

ECD changes the strength of competition (α)

In Lotka–Volterra models, the strength of competition α is a parameter that represents the per capita effects of one species on another. ECDs could either increase or decrease the strength of competition if they alter resource availability, the timing of events, or species behavior. For example, climate change can result in the extension of the growing season for plants, which could allow plants to reduce direct competitive interactions if some take advantage of the earlier growing season (Schwinning & Kelly, 2013). Similarly, if ECDs like pollution alter the foraging locations or times of species differentially, then direct competition can be reduced, enhancing coexistence, or increased, destabilizing coexistence (Bláha et al., 2019). Increased stress by ECDs can reduce competition strength as predicted by the stress gradient hypothesis (Bertness & Callaway, 1994). Decreases in the per capita competition strength mean that species are less impacted by other species and will obtain equilibrium abundances closer to their carrying capacities, thus increasing community abundance. Increasing the strength of competition will cause decreases in community abundance and therefore reduce ecosystem function (Figure 2A).

If ECDs impact competitive inequalities, notably by enhancing existing trade-offs or competitive hierarchies,

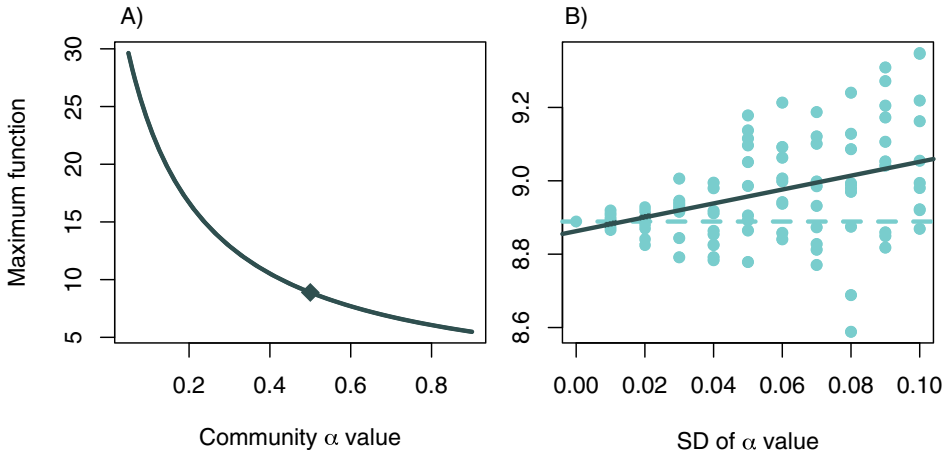

FIGURE 2 (A) The relationship between maximum function and increasing but invariant α (all species have equal competitive effects), and the diamond indicates the mean α value used in B. (B) Effect of increasing the variation in α on maximum function. The dashed line indicates the mean α (diamond in A). The solid line indicates the linear relationship (coef = 1.89, $p < 0.001$). The effects of α on BEF slope mirror the effects on maximum function.

this can cause a decline in function (Figure 2A). However, if species competitive responses are more idiosyncratic, with ECDs causing high and random deviations in the strength of competition, we should expect an average increase in function, but accompanied by a high variance in function (Figure 2B). ECDs altering interspecific interactions can move species from regions of coexistence to exclusion and vice versa according to coexistence theory (Figure 1C,D).

ECD decreases the mean intrinsic rate of increase (*r*)

Lotka–Volterra models (Box 1) demonstrate that ECDs that cause declines in reproduction or increase time to reproductive maturity (Jones & Reschke, 2005; Richard et al., 2021) will result in slower population growth rates, creating a longer window of time when assemblages are not at maximal biomass and hence not at maximal functioning (Figure 3A). Additionally, increasing the delay until carrying capacity is achieved allows other drivers or sources of fluctuation to influence populations, increasing the probability that maximal function is not realized.

ECD increases the mean intrinsic rate of increase (*r*)

Moderate increases in the intrinsic rate of increase across the community could result in a net positive effect where the maximal function is achieved faster with the effect of an ECD. However, substantial increases in *r* could be destabilizing (Figure 3B). In this case, the constituent populations could oscillate around their carrying capacity (May, 1976), causing the abundance of the community to exhibit high temporal variance. BEF estimates could be based on times of high or low function, resulting in inconsistency in prediction and inferences about ECD effects on function. ECDs can move multispecies systems into greater or reduced stability by affected *r* values (Ives & Carpenter, 2007).

The above five cases investigate how ECDs impact individual parameters. However, ECDs are likely to impact multiple population parameters simultaneously (e.g., *r* and *K*). ECDs that have strong negative effects will likely cause reductions in *r* and *K*, which could then have stronger impacts on BEF relationships than predicted from the effects of either parameter alone.

SCALING ENVIRONMENTAL CHANGE IMPACTS FOR MULTIPLE SPECIES

Predictions about the effects of single ECDs on simple systems (e.g., two-species assemblages above) appear straightforward and tractable. However, scaling up the effects of multiple ECDs on diverse multispecies assemblages is a much more complex endeavor, and one needs to consider several important factors.

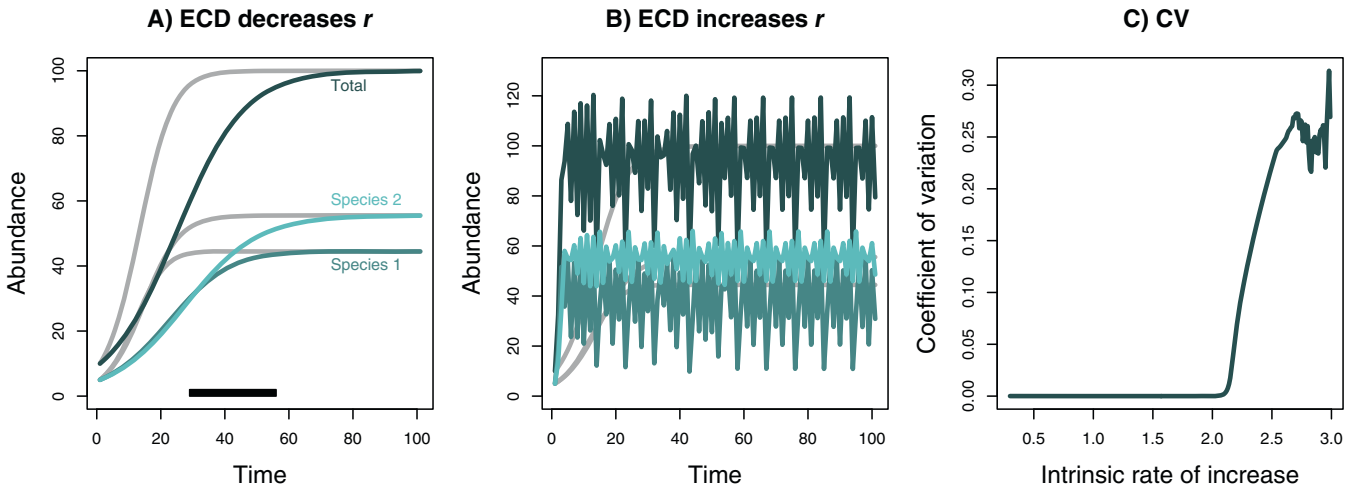

FIGURE 3 Two-species discrete-time Lotka–Volterra simulations revealing how (A) decreases or (B) increases in intrinsic rates of increase (*r*) affect community abundance and how (C) stability (measured as CV) is influenced by *r*. The gray population curves in A and B show two-species growth curves, and their summation, for the same set of parameters ($r_1 = 0.2$, $r_2 = 0.18$, $N_1 = 5$, $N_2 = 5$, $\alpha_{12} = 0.1$, $\alpha_{21} = 0.1$, $K_1 = 50$, $K_2 = 50$). The colored curves in A depict *r* values being halved ($r_1 = 0.1$, $r_2 = 0.09$), and the black bar represents the amount of time functioning was reduced. The curves in B show populations with increased *r* values ($r_1 = 3$, $r_2 = 2$). The graph in C shows the CV in total abundance with r_1 ranging from 0.3 to 3 and $r_2 = r_1 \times 0.8$, and CV is estimated after 40 time steps.

In the previous sections, we examined how changes in population parameters influenced two-species systems to make inferences about how parameter changes will affect coexistence and the cumulative abundance. Here, we now focus our attention on BEF relationships per se. The lessons from the two-species systems translate directly onto multispecies assemblages if the ECD effects are consistent across species. For example, an ECD having consistent effects across species K values as either an enrichment or a stressor will have very predictable effects. In the case of enrichment, if species coexist, the effect of the ECD on the BEF relationship will increase its intercept. The converse is true with decreasing K, where declines without altering other aspects of population dynamics will lower community abundance and result in a decrease in the BEF intercept.

The greater the number of species in an assemblage, the more likely it is that ECDs have more diverse effects on population parameters. For example, we might see greater variation in a single parameter with more species; like, greater variation in competitive effects with more species, which results in greater variance in function (Figure 2B), perhaps resulting in the appearance of inconsistent effects of ECDs on BEF relationships. Furthermore, one species could experience a reduction in r and another an increase in K, which necessarily creates more possible outcomes for BEF relationships. Some pairs of species might experience greater fitness equivalency, and for others, the result could be a greater fitness difference, resulting in a reorganization of both coexistence and species contributions to ecosystem function.

The responses of different species to ECDs can appear as trade-offs that can change competitive effects and coexistence. ECDs that are alterations of existing important environmental factors, for example, temperature, precipitation, or nutrient regimes, could accentuate existing trade-offs and result in more variable responses. In this case, where ECDs influence existing environmental factors, it is likely that some species in high-diversity assemblages will be able to compensate for those that are negatively impacted by the ECD because species are more likely to exhibit natural trade-offs to these drivers. Conversely, some ECDs will be novel, and species lack the requisite adaptations to respond to these (e.g., heavy metal or petrochemical pollution), and so these ECDs should have more consistent and negative effects across the assemblage and result in declining BEF relationships (i.e., reduced slope and intercept of the BEF relationship).

ECDs have a variety of effects on BEF relationships, from acting as stressors that strongly reduce ecosystem functioning to enriching agents that enhance species contributions to function. The divergent conclusions from studies of ECD effects on BEF (see recent meta-analyses: Hong et al., 2022; Rillig et al., 2023) are likely influenced by differences in how ECDs impact individual species and the magnitude and variance of these impacts at the community scale. BEF relationships under ECDs can differ from ambient and benign BEF patterns in a myriad of ways but can be described by changes in the intercept and slope of the BEF relationship.

These divergent effects of ECDs can be measured according to their mean effect on population parameters and the variation in this effect (Figure 4). Here, we use simulations based on multispecies Lotka–Volterra models to assess the effects of ECDs on BEF relationships. Communities at equilibrium and the resulting ecosystem functioning are estimated using the Lemke–Howson algorithm (Serván et al., 2018). We start with communities with one to eight species, where all species have $K = 5$ and $\alpha_{ij} = 0.5$. We then apply an effect of ECDs by changing the mean and variance of these two parameters among the set of species and then plot the BEF relationship, where function is the summation of abundances (Figure 4A). Figure 4 presents predicted BEF relationships resulting from changes in α (Figure 4B,C), changes in K (Figure 4D–F), and changes in both α and K (Figure 4G–I).

Increasing the strength of competition results in a lower BEF slope (Figure 4B), while weakening competition results in a higher BEF slope (Figure 4C). Stressors that decrease K for all species cause a decline in the intercept of the BEF relationship (Figure 4D–F), but a large variance in the effect on K can buffer the impact on function at high diversity (Figure 4F). While ECDs that enrich communities by increasing K for all species result in an increase in the intercept or slope of the BEF relationship (Figure 4G–I).

The eight classes of the predicted BEF relationships under ECDs (Figure 4B–I) make clear the links between the intercept and slope of the BEF relationship and the population parameters, namely the mean interaction strength among species (α) and the mean and variance in carrying capacity (K) among species. We first see that a change in mean α, on its own, only decreases (Figure 4B) or increases (Figure 4C) the slope, without affecting the intercept. These types of changes in functioning should be strongly tied to the complementarity effect, as they are driven by reduced niche overlap that is irrespective of species' performance in monocultures. Second, a change in mean K, by itself, decreases (Figure 4E) or increases (Figure 4I) both the slope and intercept, highlighting a case where a community wide limiting resource is increased (e.g., nitrogen deposition). Last, an increased variance in K increases the slope (Figure 4D,F). Such an increase in functioning should be largely explained by

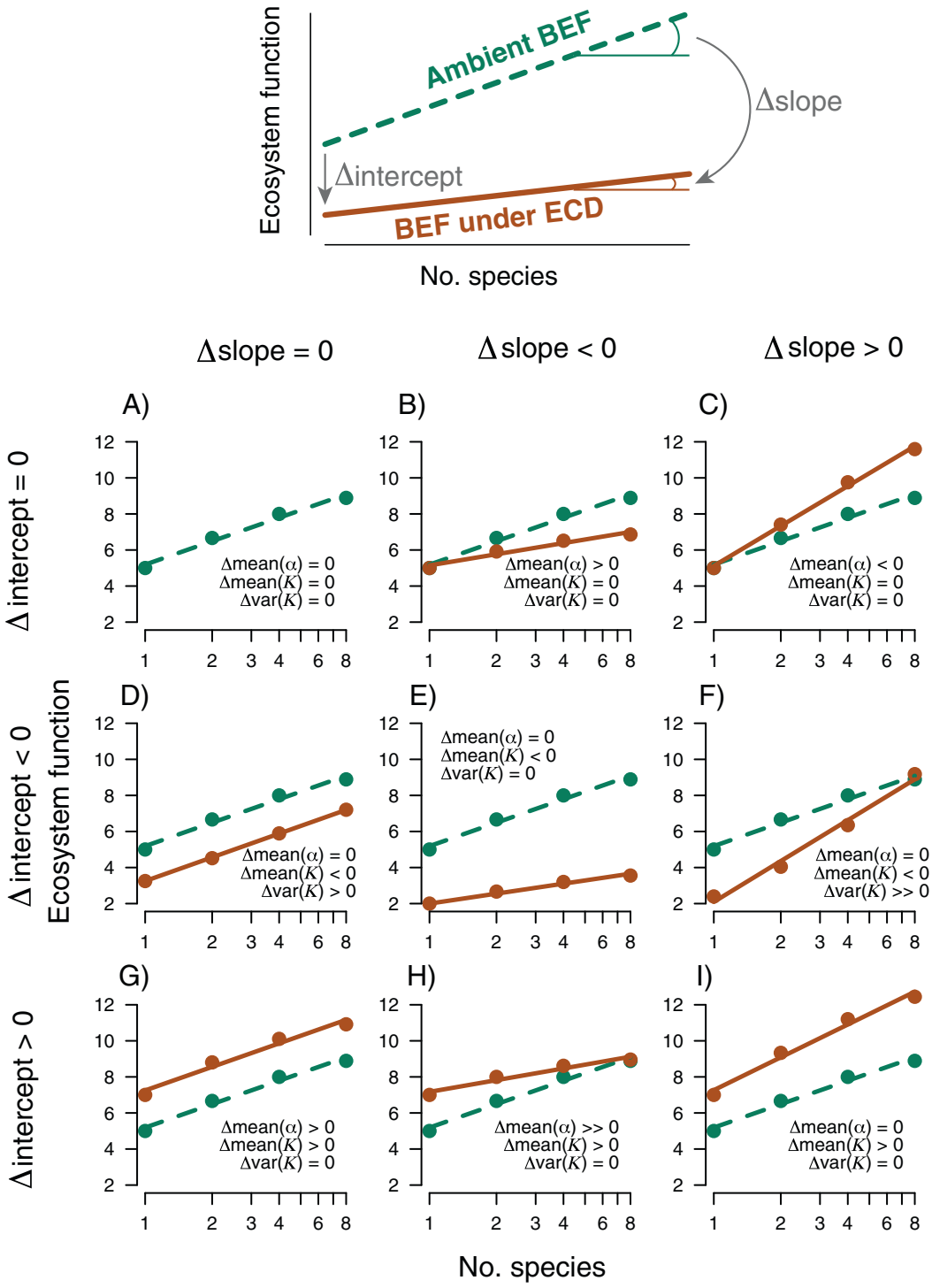

FIGURE 4 Biodiversity-ecosystem function (BEF) relationships predicted using the generalized Lotka–Volterra model in which an environmental change driver (ECD) was assumed to impact the mean interaction strength among species (α) and the mean and variance in carrying capacity (K) among species, shown within each panel. The results of ECD effects on these population parameters can cause increases or decreases in the BEF intercept and slope, here measured as $\Delta = \text{BEF}_{\text{ECD}} - \text{BEF}_{\text{Ambient}}$. The abundances of the equilibrium community were estimated using the Lemke–Howson algorithm, and ecosystem function is the summation of these abundances. The ambient BEF curve is generated with all species having $\alpha = 0.5$ and $K = 5$.

selection effect, given the expected pronounced covariance in species' performance between monocultures and mixtures.

Differing inferences about the effect of ECDs on diversity and function (e.g., Hong et al., 2022; Rillig et al., 2023) are potentially explained by different effects of ECDs.

Hong and colleagues highlighted the fact that some studies reported increases in BEF slopes under ECDs. Although they did not assess intercepts explicitly, the ECDs they considered are likely to either enrich or enhance species trade-offs. They considered ECDs such as temperature, moisture, CO_2, and nutrient addition, all of which are variable factors that species would naturally deal with and might already have evolved trade-offs promoting spatial or temporal coexistence. This is reinforced by the fact that they observed increases in complementarity effects. However, Rillig et al. (2023) analyzed experiments examining the effects of anthropogenic stressors on function, such as heavy metal contamination, increasing salinity, changes in pH, and human influences such as urbanization. These ECDs are much more likely to have negative effects and affect species in novel ways that fall outside of evolved trade-offs. Thus, given the nature of the ECDs investigated, it is reasonable to expect that combinations of ECDs that are enriching or play on existing natural trade-offs (e.g., Hong et al., 2022) will likely conform to the predictions shown in Figure 4C,F,G,I. The novel stressors that result in more consistent negative effects on species should result in the relationships depicted in Figure 4B,D,E.

ENVIRONMENTAL CHANGE IMPACTS ON BEF RELATIONSHIPS UNDER REALISTIC SCENARIOS

The mechanistic framework presents a relatively simple example relying on some important assumptions, such as no feedback between function and ECDs, or about how the level of function is an outcome of community abundance. Even with our simplifying assumptions, it is clear that a diversity of ECD effects on BEF relationships is possible (Figure 4). Although divergent ECD effects would seem to invite an inference of context dependency (Catford et al., 2021), the reality, like with most cases of context dependency, is that there are mechanistic reasons underlying divergent effects of ECDs on BEF relationships (De Laender et al., 2016). Furthermore, empirical studies that carefully manipulate diversity and ECDs are desperately needed if we are to provide managers and policy makers with sound advice on how to use diversity in restoration and green infrastructure to enhance function and service delivery.

Moving forward, beyond accumulating experimental evidence, we also need to consider several important extensions of this framework to realistic scenarios.

Case 1: BEF-ECD feedback

One of our assumptions is that ECDs impact BEF relationships in a single direction. However, it is important to consider that there might be a bidirectionality to this relationship (Figure 5, Case 1). That is, greater functioning might cause a decrease in the effect of the ECD (e.g., Jia et al., 2020). For example, plant biomass can provide a sink for heavy metals contaminating soil (Chirakkara & Reddy, 2015; Evangelou et al., 2015), and so high-diversity plantings that result in high plant biomass could reduce soil pollution compared with less diverse plantings (Jia et al., 2020).

As a strategy for soil remediation, resistant or hyperaccumulating plants (Sytar et al., 2021) could be selected to enhance local diversity and hence local biomass production at contaminated sites.

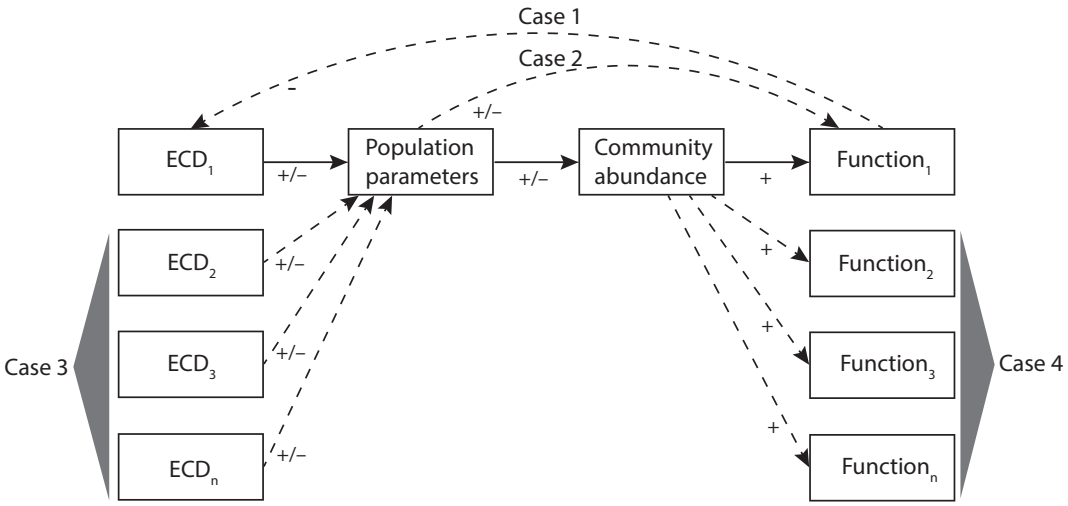

FIGURE 5 The pathway of effect for environmental change drivers (ECDs) on Biodiversity-ecosystem function (BEF) relationships, including four complicating pathways (Cases 1–4), discussed in *Environmental change impacts on BEF relationships under realistic scenarios*.

Case 2: Function not correlated with community abundance

In our simulations, we assumed that function was directly proportional to biomass, which is the case for function directly tied to coexistence (Turnbull et al., 2016). However, we could model functions that depend more directly on species traits, where the presence of a specific trait has strong effects on function independent of community abundance (Cadotte et al., 2017) as depicted in Figure 5, Case 2. For example, pollination services could be greatly improved by the presence of a late-season flowering plant in Asteraceae in a field dominated by grasses. In this case, we could model the presence or abundance of individual species and make inferences on changes to function. ECDs that impact competitive exclusion through effects on *K* could have strong direct effects on function.

Case 3: Predicting the effect of multiple ECDs on BEF relationships

In our simulations, we examined the effect of a single ECD on BEF relationships under different scenarios of effect, but considering multiple ECDs could create more complex outcomes (Figure 5, Case 3). This will especially be relevant when different ECDs have differing mean effects and variances in that effect across species. Multiple ECDs could be compounding (causing greater declines in BEF relationships) or creating new trade-offs that could strengthen BEF relationships. More work is needed to fully understand and predict the effect of multiple ECDs.

Case 4: Predicting ECD effects on multiple functions

In our simulations, we only considered a single function, but multiple ecosystem functions, or multifunctionality, are undoubtedly important in real landscapes. There are many methods that permit the statistical combining of multiple functions to assess how biodiversity affects multifunctionality (Byrnes et al., 2014; Chao et al., 2024; Mori et al., 2023). How ECDs impact multifunctionality will depend on whether functions covary and the consistency of ECD effects (Figure 5, Case 4), especially on abundant versus rare taxa (Du et al., 2024). If the measured functions all have a direct relationship with community abundance, then they are likely to correlate with one another. If the pathway of effect is as depicted in Figure 5, where the ECD effects manifest as changes in community abundance which cascade to functions correlated with abundance, then we should expect that the effect on multifunctionality is predicted by the mean and variance of the ECD effects on species' *K*. For example, if the combined effects of all ECDs are a significant decrease in *K* with relatively low variance among species, multifunctionality should be negatively impacted. If, instead, there is a large variance in ECD effects, there might be emergent trade-offs among functions. It could be that the strongest ECD that negatively affects *K* and function will simply set the limit that the measured multifunction could achieve, which would be apparent with multifunctionality analyses that employ a threshold approach (Rillig et al., 2023).

From experimental plots to natural systems

The approach used in this paper is meant to assist with the development of hypotheses and sophisticated inference for local-scale manipulative experiments because increasing numbers of studies have been published that manipulate both diversity and some ECD (e.g., see Hong et al., 2022). Expanding this approach to ECD effects in natural systems is undoubtedly a complicated endeavor because of the confounding effects of underlying factors that covary with diversity gradients. Despite results showing that BEF relationships are perhaps even stronger in natural systems (Flombaum & Sala, 2008), the reality is that species that contribute most to function might simply be the most abundant, and depending on the nature of antagonistic interactions and nutrient co-limitation, ECDs can cause species loss and enhanced functioning simultaneously, resulting in weakened or negative BEF relationships (Cadotte et al., 2017; Dee et al., 2023; Hagan et al., 2021; Wassen et al., 2005). A next step would be to include environmental gradients, other antagonistic interactions, and direct effects on function not mediated by coexistence to examine more diverse impacts of ECDs on function.

Further, scaling up ECD effects on biodiversity and function in natural assemblages requires the incorporation of spatial and temporal dynamics that influence coexistence. It is often recognized that small-scale coexistence experiments underpredict coexistence because they miss the effects of source-sink dynamics associated with spatial heterogeneity and temporal niches (Kraft et al., 2015), or that artificial diversity manipulations override the natural filters that structure local diversity and function (Hagan et al., 2021). There is a clear need to incorporate these meta-community processes (Gonzalez et al., 2020; Thompson et al., 2020) to make better predictions about

local diversity, function, and the across-scale responses to ECDs (Firkowski et al., 2022; Zelnik et al., 2024).

CONCLUSIONS

Here, we show, with a series of relatively simple simulations, that ECDs that influence population parameters (*r*, *K*, and α) can result in substantial alterations of BEF relationships. Perhaps more importantly, these effects can result in a large diversity of changes to BEF relationships, either increasing or decreasing both the intercept and slope of the BEF curve. These effects depend on both the magnitude of the effect of ECDs on population parameters and the variance of the effect between species. The accumulation of additional empirical data on the impacts of ECD on communities and ecosystems is critically important, and furthermore, we need to combine such empirical studies with mechanistic models based on ecological theory. Thankfully, methods for estimating parameters of such models using empirical data have seen important advances recently (e.g., Maynard et al., 2020) and forward the general call for a more theoretical approach to predicting ECD impacts on ecosystem function (De Laender, 2018; De Laender et al., 2016; Mensens et al., 2015; Spaak et al., 2017). Such process-oriented approaches provide generalized and predictive understanding to guide biodiversity conservation, restoration, and green infrastructure design under environmental change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code (Cadotte, 2025) is available on Zenodo: https://zenodo.org/records/14790142.

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