










LETTER

Mean species responses predict effects of environmental change on coexistence

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Abstract

Environmental change research is plagued by the curse of dimensionality: the number of communities at risk and the number of environmental drivers are both large. This raises the pressing question if a general understanding of ecological effects is achievable. Here, we show evidence that this is indeed possible. Using theoretical and simulation-based evidence for bi- and tritrophic communities, we show that environmental change effects on coexistence are proportional to mean species responses and depend on how trophic levels on average interact prior to environmental change. We then benchmark our findings using relevant cases of environmental change, showing that means of temperature optima and of species sensitivities to pollution predict concomitant effects on coexistence. Finally, we demonstrate how to apply our theory to the analysis of field data, finding support for effects of land use change on coexistence in natural invertebrate communities.

KEYWORDS

climate change, community ecology, environmental ecology, environmental stressors, food chains, food webs, global change, pollution

INTRODUCTION

Understanding how environmental change affects community and ecosystem variables is a prerequisite to effective conservation (Orr et al., 2020). One approach is

to study effects of a specific environmental driver (e.g., temperature or pollution) on a specific community (Urban et al., 2021). However, it is logistically challenging to apply this approach to every single combination of environmental driver and community (O'Hara

et al., 2021). An important question is therefore whether we can achieve an understanding that transcends specific drivers and specific ecological communities (De Laender, 2018; Simmons et al., 2021). Theoretical ecology has a rich history of transcending specifics and uncover more general principles of community behaviour. While idiosyncrasy and context dependence at the population level can be overwhelming, a handful of summary statistics (e.g., the interspecific variance of the carrying capacity Barbier et al., 2018), or the average strength of density-dependence (Barabás et al., 2017) often predict a community's fate. These statistics summarise (across species) how populations grow and permit predicting community behaviour without information on each and every species. Environmental change typically elicits species responses that will change population growth (Cenci et al., 2018; Chesson, 2000; De Laender, 2018; Pásztor et al., 2016; van Nes & Scheffer, 2004). It is therefore worthwhile asking whether summaries of species responses to environmental change are sufficient to produce generic patterns of community change.

An important manifestation of community change is compositional change (Dornelas et al., 2014; McGill et al., 2015; Spencer, 2015; van Nes & Scheffer, 2004), which happens when a given set of species ceases to coexist. Theoretically speaking, a necessary condition for coexistence is that all species realise a positive population density. Using a community model, one can quantify the scope for coexistence by computing the proportion of parameter settings, out of all possible ones, that allow for coexistence (Grilli et al., 2017; Logofet, 2009; Saavedra et al., 2017; Song et al., 2018). This proportion is called the *feasibility domain*, and it is equivalent to the

probability of all species simultaneously achieving a positive population density, assuming that each parameter setting is equally likely. In many applications, including this work, a 'parameter setting' is a given combination of the species' intrinsic growth rates. Consequently, feasibility is measured by computing how many of such combinations admit positive population density for all species (Figure 1).

Species interaction coefficients fully determine the feasibility domain: both the overall strength of interspecific interactions and the interaction network (i.e., who interacts with whom) influence the size of the feasibility domain (Cenci et al., 2018; Grilli et al., 2017; Saavedra et al., 2017) (Figure 1, left panel). Species responses to environmental change can modify species interactions, for example, by altering competition or consumption rates (Baert et al., 2016; Edwards et al., 2015; Uszko et al., 2017). Thus, such effects can shrink or expand the feasibility domain, which can lead to loss of coexistence (Figure 1, right panel). However, in addition to changing how species interact, species responses can also modify intrinsic growth rates (Baert et al., 2016; Edwards et al., 2015; Uszko et al., 2017). Ignoring such effects can lead to wrong predictions of coexistence: growth rate combinations that permit coexistence when only species interactions are affected may cease to do so when environmental change alters the growth rate combination itself. For instance, if environmental change not only alters the feasibility domain but also changes growth rate combinations, coexistence may be unexpectedly lost or maintained. Therefore, a general understanding of environmental change effects on coexistence demands accounting for two kinds of species responses: those that

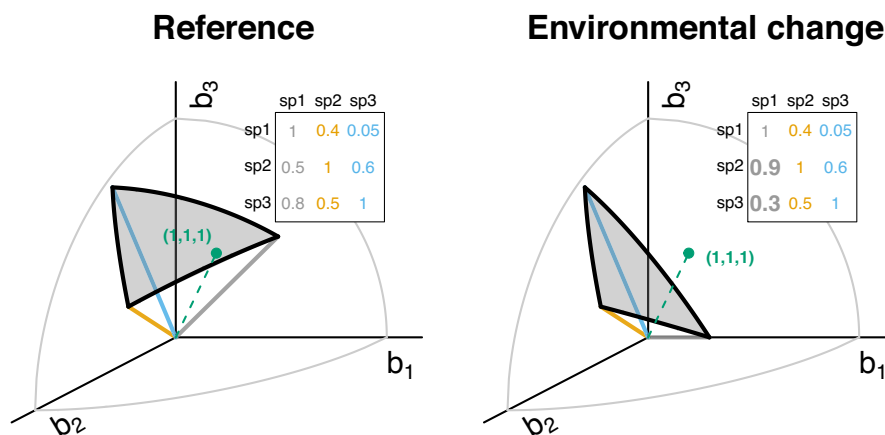


FIGURE 1 Conceptualising (loss of) coexistence under environmental change, using a three-species community as a cartoon example. Left panel: The feasibility domain (in grey) is fully determined by the matrix of species interactions (top right inset). Specifically, the columns of this matrix dictate the directions of the feasibility domain's boundaries (in light grey, orange and blue). These boundaries delimit the possible intrinsic growth rate combinations (here b_1 , b_2 , b_3 , since there are three species) that make the densities of all species positive: the feasibility domain is the collection of all these combinations of b_i . Specifically, if the *direction* of an intrinsic growth rate combination crosses the feasibility domain, as is the case in the example $b_1 = b_2 = b_3 = 1$ (green), all species coexist. Right panel: When environmental change affects species interactions (here, effects of species 1 on species 2 and 3, in bold), the boundaries - and therefore the feasibility domain—can change as well. As a result, directions of growth rate combinations accommodating coexistence under reference conditions can now cease to do so: for example, $b_1 = b_2 = b_3 = 1$ does not cross the feasibility domain anymore, meaning coexistence is lost for that combination.

modify species interactions, and those that modify intrinsic growth (Song et al., 2020).

Here we incorporate species responses that modify species interactions, and those that modify intrinsic growth, into the feasibility framework and ask how these responses predict effects on coexistence. We first carry out mathematical analyses on both small and very large bi- and tritrophic communities and then carry out simulations in communities of intermediate size. Both approaches support the same conclusion: we do not need responses of every species; mean responses across species within a trophic level predict concomitant changes of coexistence. Next, we benchmark our theoretical findings by using two relevant cases of environmental change, temperature change and pollution. More specifically, we show that summaries of temperature optima and inflection points of the Hill equation for pollutants suffice to predict effects on coexistence (Ritz, 2010; Uszko et al., 2017). Finally, we demonstrate how to apply the theoretical framework to test for the effects of environmental change on coexistence using a common type of biomonitoring dataset. Such datasets typically contain observations of community composition and proxies of environmental change across sites in a landscape (Daskalova et al., 2020; Malaj et al., 2014; Outhwaite et al., 2020). Within the framework we use here (Figure 1), we propose that sites with different local conditions can be defined as different intrinsic growth rate combinations (Figure 2). That is because different local conditions can lead to different intrinsic growth rates. Thus, a decrease (resp. increase) of a community's feasibility domain implies that this focal community will persist across fewer (resp. more) sites with different local conditions. This 'spatial' interpretation of the feasibility domain size makes two implicit assumptions, however. First, it rules out mass effects whereby species persist through dispersal, despite inappropriate local environmental conditions (Leibold et al., 2004). Second, it assumes that local environmental conditions *only* influence intrinsic growth rates. Indeed, by its very definition, species interactions are constant across locations in Figure 2. Thus, it is not obvious if this spatial interpretation holds when species are able to disperse and local conditions influence species interactions. We, therefore, use a metacommunity model to confirm that dispersal and locally varying interactions (which our theory ignores) do not influence our theoretical predictions. After this confirmation, we then use our spatial interpretation of the feasibility domain size to analyse observations of macroinvertebrate communities in US streams exposed to varying degrees of human pressure. Streams are key contributors to aquatic biodiversity, while at the same time threatened by changes associated with human activity (Reid et al., 2019; Vörösmarty et al., 2010), including environmental pollution (Malaj et al., 2014). The results of this last analysis suggest a lower feasibility domain size across human-altered sites.

METHODS

Feasibility

We consider bi- and tritrophic communities where the dynamics of population densities n_i obey

$$\frac{dn_i}{dt} = n_i \left(b_i(\epsilon) + a_{ii}n_i + \sum_{j \neq i} a_{ij}(\epsilon)n_j \right), \quad (1)$$

where $b_i(\epsilon)$ is the intrinsic growth rate (> 0 for resources; < 0 for consumers and predators, representing mortality), a_{ii} is the intraspecific interaction and $a_{ij}(\epsilon)$ is the interspecific interaction, that is, the strength of consumption/predation: $a_{ij}(\epsilon) < 0$ if j feeds on i ; $a_{ij}(\epsilon) > 0$ if i feeds on j ; $a_{ij}(\epsilon) = 0$ if there is no feeding link. Intrinsic growth and interspecific interactions that differ from zero depend on a single environmental change ϵ :

$$\begin{aligned} a_{ij}(\epsilon) &= a_{0,ij} \alpha_i(\epsilon) \alpha_j(\epsilon), \text{ with } j \neq i, \\ b_i(\epsilon) &= b_{0,i} \beta_i(\epsilon) \end{aligned} \quad (2)$$

where the parameter values in the absence of environmental change ($a_{0,ij}$, $b_{0,i}$) get multiplied with functions that return the effect of environmental change ($\alpha_i(\epsilon)$, $\alpha_j(\epsilon)$ and $\beta_i(\epsilon)$). Throughout all analyses, we set $\alpha_i(\epsilon) = 1$ when i is being eaten by j , and $\alpha_j(\epsilon) = 1$ when j is being eaten by i . This means that the environmental change affects species interactions by affecting the feeding rate of the consumer or predator (i.e., the antagonist). Henceforth, we refer to effects on the antagonist as $\alpha_j(\epsilon)$. Values of $\alpha_j(\epsilon)$ and $\beta_i(\epsilon)$ less than 1, exactly 1 and greater than 1 mean a negative effect, no effect and a positive effect on the parameter respectively. Logically, $\alpha_j(0) = 1$ and $\beta_i(0) = 1$: no change implies no effect. Examples of such multiplicative effects include acidification effects on colonisation rates in corals (Anthony et al., 2011, their equation 5), pollutant effects on intrinsic growth rates and carrying capacities of producers (De Raedt et al., 2019, their Equation 1) and temperature effects on both intrinsic growth and consumption (Uszko et al., 2017, their equation 1).

A species' density is at equilibrium when $dn_i/dt = 0$. If this equilibrium n_i^* is strictly positive, it obeys $0 = b_i(\epsilon) + a_{ii}n_i^* + \sum_{j \neq i} a_{ij}(\epsilon)n_j^*$. This equation can be cast into matrix notation:

$$\mathbf{0} = \mathbf{b} + \mathbf{A}\mathbf{n}^*, \quad (3)$$

where the vectors $\mathbf{0}$, \mathbf{b} and \mathbf{n}^* contain, respectively, all zeros, the intrinsic growth rates and the equilibrium population densities. The matrix \mathbf{A} contains the species interactions (inter- and intraspecific interactions). Because the environmental change effects are multiplicative, we can write $\mathbf{b} = \beta \mathbf{b}_0$, where β is a diagonal matrix containing all $\beta_i(\epsilon)$ along its diagonal, and \mathbf{b}_0 contains all intrinsic growth rates $b_{0,i}$ without environmental change. Solving Equation 3 for \mathbf{n}^* yields the equilibrium

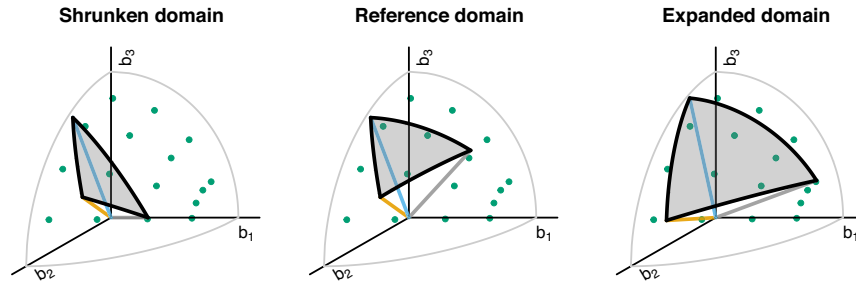


FIGURE 2 Spatial interpretation of the feasibility domain. Sites with different local conditions located across a landscape can be plotted as different intrinsic growth rate combinations (dots). If the feasibility domain shrinks (left vs. middle), we expect to see a reduction in the number of distinct local conditions where a focal community is found. Conversely, if the domain expands (right vs. middle), we anticipate seeing an increase in the number of distinct local conditions.

Symbol	Meaning
ϵ	amount of environmental change ($\epsilon = 0$ means no change)
\mathbf{A}	matrix containing consumption and predation rates of j on i , $a_{ij}(\epsilon)$
\mathbf{A}_0	matrix containing consumption and predation rates of j on i in absence of environmental change, $a_{0,ij}$
\mathbf{b}	vector containing intrinsic growth rates of i , $b_i(\epsilon)$
\mathbf{b}_0	vector containing intrinsic growth rates of i in the absence of environmental change, $b_{0,i}$
$\alpha_j(\epsilon)$	effect on species j 's consumption or predation rate, a function of ϵ
$\beta_i(\epsilon)$	effect on species i 's intrinsic growth rate, a function of ϵ
α	diagonal matrix with the $\alpha_j(\epsilon)$ on its diagonal
β	diagonal matrix with the $\beta_i(\epsilon)$ on its diagonal
r_{α_j}	linear response of species j 's consumption or predation to environmental change $\partial\alpha_j / \partial\epsilon$
r_{β_i}	linear response of species i 's intrinsic growth to environmental change $\partial\beta_i / \partial\epsilon$
Ξ	size of the feasibility domain
δ	quantity proportional to the mean responses r of resources and consumers
ζ	quantity proportional to the mean responses r of resources, consumers and predators

TABLE 1 The recurring symbols used in this article. Boldface indicates vectors or matrices; other symbols are either scalars or functions.

$$\mathbf{n}^* = -\mathbf{A}^{-1}\beta\mathbf{b}_0 = -(\beta^{-1}\mathbf{A})^{-1}\mathbf{b}_0 \quad (4)$$

The matrix product $\beta^{-1}\mathbf{A}$ can be understood as *effective species interactions*: interactions that will account for effects on intrinsic growth (contained in β), and species interactions plus the environmental effects thereon (contained in \mathbf{A}). This matrix product fully determines the *feasibility domain size*, which we define here as the range of intrinsic growth rates prior to environmental change (contained in \mathbf{b}_0) such that all entries of \mathbf{n}^* are positive. The matrix \mathbf{A} differs between bi- and tritrophic communities but always depends on \mathbf{A}_0 (the species interactions without environmental change) and α (the diagonal matrix containing all $\alpha_j(\epsilon)$ along its diagonal; Data S1, Section 1.1.1). Table 1 lists all recurring symbols used in the main text.

Note that only the relative magnitudes of \mathbf{b}_0 's elements matter: if some \mathbf{b}_0 leads to a positive \mathbf{n}^* , then so will any multiple of \mathbf{b}_0 (Grilli et al., 2017). For example,

if $(\beta^{-1}\mathbf{A})^{-1}\mathbf{b}_0 > 0$, then so will $(\beta^{-1}\mathbf{A})^{-1}m\mathbf{b}_0 > 0$, where $m > 0$ is any scalar.

Feasibility does not guarantee local asymptotic dynamical stability in general. In our case however, one can give a proof that feasible systems are also locally stable (Data S1, Section 1.1.2). We therefore never need to worry about the existence of feasible but unstable equilibria, which may give the illusion of coexistence without truly allowing for it.

Analyses

The objective of our analyses was to explore how a small environmental change ϵ affects the feasibility domain size, hereby denoted by Ξ . We carried out two types of analyses using closed-form expressions that calculate Ξ from the matrix of effective interactions $\beta^{-1}\mathbf{A}$. In a first set of analyses, we considered communities of three species, using the analytic expression derived by Gourion

and Seeger (2010) (Data S1, Section 1.2.1). In the bi-trophic community, species 1 and 2 were resources on which species 3 fed equally: $a_{0,13} = a_{0,23} \equiv a_{0,3}$. In the tritrophic community, species 1, 2 and 3 were resource, consumer (feeding at $a_{0,2}$) and predator (feeding at $a_{0,3}$) respectively. In a second set of analyses, we considered very large bitrophic and tritrophic communities, using the analytic expression derived by Grilli et al. (2017) (Data S1, Section 1.2.2). We carried out both analyses for bi- and tritrophic communities by using the appropriate expression for \mathbf{A} (Data S1, Section 1.1.1). We set a_{ii} to -1 for resources and to 0 for consumers and predators (if present). We further assume ε to be small enough for $\beta_i(\varepsilon)$ and $\alpha_j(\varepsilon)$ to be linear in ε , as done previously (van Nes & Scheffer, 2004): $\beta_i(\varepsilon) = 1 + r_{\beta_i}\varepsilon$ and $\alpha_j(\varepsilon) = 1 + r_{\alpha_j}\varepsilon$, where r_{β_i} and r_{α_j} are the responses of intrinsic growth rate and consumption rate respectively. This yielded an expression for the feasibility domain size (Ξ) as a function of environmental change ε . We then took the derivative $d\Xi/d\varepsilon$ at $\varepsilon = 0$ to quantify the effect of environmental change on feasibility domain size. We then explored how this effect depended on the species responses r .

Simulations

Our objective was to test whether the relationship between species responses r and effects on Ξ , as established using analyses for either very small or very large communities, holds for communities of intermediate size (i.e., where species richness is larger than three but smaller than several dozens) and when allowing weak competition among resources. To this end, we ran simulations using appropriate methods (Song et al., 2018), and following the simulation protocol in Data S1, Section 1.3. Briefly, we first computed Ξ without environmental change but for various combinations of consumption and predation rates and community size (number of species). We then considered a subset of those combinations for which Ξ was not too small. We then randomly sampled effects on intrinsic growth, consumption and predation, and calculated Ξ again. The ratio of Ξ with and without environmental change quantified the effect of environmental change on Ξ . We then evaluated if the relationship of this ratio to the species responses r was qualitatively similar to the analytical results.

We performed all simulations in R (R Core Team, 2016; Soetaert et al., 2010) and Python (Virtanen et al., 2020) with the reticulate package (Allaire et al., 2017). Code is available in https://github.com/fdelaend/De_Laender_et_al_feasibility.

Application to temperature change and pollution

Our objective was to link the analytical results (relationship between species responses r and $d\Xi/d\varepsilon$) to two

practical examples for the case of a bitrophic community with weak consumption. To this end, we used available functional forms for $\beta_i(\varepsilon)$ and $\alpha_j(\varepsilon)$ to obtain species responses r_{β_i} and r_{α_j} .

For a temperature change ΔT , $\varepsilon = \Delta T$ and so species responses at small ε are $r_{\beta_i} = (\partial\beta_i(\Delta T)/\partial\Delta T)|_{\Delta T=0}$ and $r_{\alpha_j} = (\partial\alpha_j(\Delta T)/\partial\Delta T)|_{\Delta T=0}$. Functional forms of $\beta_i(\varepsilon)$ and $\alpha_j(\varepsilon)$ for temperature were taken from Uszko et al. (2017). These functions contain parameters such as temperature optima and niche widths (Data S1, Section 1.4).

For a pollutant concentration c , we set the reference condition to be ‘not polluted’ ($c = 0$). Therefore, $\varepsilon = c$. Then, $r_{\beta_i} = (\partial\beta_i(c)/\partial c)|_{c=0}$ and $r_{\alpha_j} = (\partial\alpha_j(c)/\partial c)|_{c=0}$. Functional forms of $\beta_i(\varepsilon)$ and $\alpha_j(\varepsilon)$ for pollutants are typically Hill functions and were taken from Ritz (2010). These functions contain as a parameter the inflection point (the intensity at which the parameter changes fastest with c ; Data S1, Section 1.4).

Application to field data

Our theory ignores dispersal and assumes that species interactions are constant across all sites in a landscape (Figure 2). Hence, it is unclear if application to monitoring datasets is warranted (see *Introduction*). We therefore first examined if adding dispersal and locally varying interactions would impair the capacity of species responses to predict the number of distinct sites in which a community persists. To do so, we ran simulations with a metacommunity model (Data S1, Section 1.5.1) that explicitly accounts for these two mechanisms. Specifically, we simulated dynamics across sites with distinct intrinsic growth rate combinations, and measured persistence across these sites. We measured persistence as the fraction of sites where the focal community is able to persist. We did this with and without environmental change and tested if species responses predicted the resulting effect on persistence across sites.

We then carried out an analysis of a large monitoring dataset to illustrate how to explore effects of environmental change on coexistence, using the spatial interpretation of the feasibility domain (Figure 2). Ideally, one would measure how much intrinsic growth rates vary, and compare this variation between a reference landscape (Figure 2, middle panel) and a landscape subject to environmental change (Figure 2, left or right panel). However, local intrinsic growth rates are typically unknown, so one cannot test if different sites in which the same community is found effectively represent distinct growth rate combinations. We, therefore, opted for an alternative approach, which measures the range of local environmental conditions along which a community is observed. We will call this range the *used range*, as it can be thought of as the range of local conditions ‘used’ by the community. One can then compare

the *used range* across reference sites (touched less by human activity) and across sites altered more by human activity to evaluate if human activity affects coexistence (sensu feasibility). Based on our theoretical results (environmental change affects feasibility domain size), one expects different used ranges across reference sites than across altered sites. Note that this analysis is based on two assumptions: (1) sites with more different local environmental conditions will also represent more different intrinsic growth rate combinations (i.e., are located further apart on the sphere in Figure 2); (2) communities are not able to persist beyond the range of environmental conditions observed across all sites (here called the ‘available range’). While we cannot test assumption (1), a contraindication of assumption (2) would be that communities persist across the entire *available range*, making it unlikely they could not persist at other conditions as well. We therefore tested if the *used range* was consistently smaller than the *available range* for all communities that will persisted in at least three sites.

Our biological data consist of observations of macroinvertebrate densities (ind. per m² for > 500 genera) across 3902 sites along US streams, sampled between 2000 and 2019. These data were collected as part of the US Environmental Protection Agency's National Rivers and Streams Assessment (NRSA) (EPA, 2020a, 2020b). We only retained taxa that occurred in at least 10% of the sites. A full description of the data preprocessing is given in Data S1, Section 1.5.2. As a proxy for the degree of environmental change, we used the land use category of the catchment within which a site was located, using data from Hill et al. (2016). We then labelled sites that were ‘forest/wetland’, or ‘grassland/shrub’ as ‘reference’; we labelled sites that were ‘urban’ or ‘agriculture’ as ‘altered’. We assumed that ‘reference’ sites have been less exposed to human activity than ‘altered’ sites. As a proxy for local environmental conditions, we used uncorrelated water chemistry variables that we temporally and spatially matched with the biological data. A full description is given in Data S1, Section 1.5.2.

We then identified which communities were observed across at least three reference and three change sites, removing taxa from a site when it had a relative frequency below 5% at that site. For each of these, we calculated the used range (= max – min) of every chemistry variable across the reference sites in which they were found, and then did the same across the altered sites in which they were found. We then computed the logarithm of the quotient of these two *used ranges* and considered it as a response variable in a linear model with the period of sampling (2000–2005, 2005–2010, 2010–2015 and 2015–2020) and chemistry variable as categorical predictors (no interactions). We applied a Bonferroni-corrected p-value of 0.05/8 = 0.00625 to account for multiple comparisons (we had eight water chemistry variables).

RESULTS

Analyses

In bithrophic communities of three species (species 1 and 2 are resources and species 3 is the consumer), the effect of environmental change ϵ on the feasibility domain size (Ξ) depends on two terms (Data S1, Section 2.1):

$$\left. \frac{d\Xi}{d\epsilon} \right|_{\epsilon=0} = \underbrace{\left(\frac{r_{\beta 1} + r_{\beta 2}}{2} - r_{\beta 3} + r_{\alpha 3} \right)}_{\delta} h(a_{0,3}). \quad (5)$$

The first term, which we will henceforth call δ , only depends on species responses r . The second term, $h(a_{0,3})$, only depends on the consumption rate without environmental change $a_{0,3}$ (full equation in Data S1, Section 2.1). The quantity δ is the sum of (1) the mean response $(r_{\beta 1} + r_{\beta 2})/2$ of the two resources' intrinsic growth rates, (2) the negative response $-r_{\beta 3}$ of the single consumer's intrinsic growth (mortality) rate and (3) the response $r_{\alpha 3}$ of the single consumption rate. To obtain δ , one thus needs to sum the responses of the resource and of the consumer trophic levels, taking the mean response per trophic level in case it contains more than one species (in this case, the resources). The ecological meaning of δ is that environmental change types that mostly depress population growth (i.e., reduce the intrinsic growth or consumption rate, or increase mortality) will have $r_{\beta 1} < 0, r_{\beta 2} < 0, r_{\beta 3} > 0, r_{\alpha 3} < 0$, and therefore $\delta < 0$, leading to a reduction of the feasibility domain if $h(a_{0,3}) > 0$.

The second term, $h(a_{0,3})$, is positive when $0 < a_{0,3} < 1$ and negative when $a_{0,3} > 1$ (Figure S1). It therefore acts as a modifier that translates δ to the community-level. The ecological meaning of this modifier is that communities where consumption is weak ($0 < a_{0,3} < 1$) respond in an opposite way to environmental change than communities where consumption is strong (Figure 3, left panel). This cut-off value for $a_{0,3}$ (i.e., 1) corresponds to the value that maximises the feasibility domain size in the absence of environmental change (Figure S1).

For tritrophic communities of three species (species 1,2,3 are the resource, consumer and predator species respectively), the effects of environmental change on feasibility domain size appear more complicated (Data S1, Section 2.1):

$$\left. \frac{d\Xi}{d\epsilon} \right|_{\epsilon=0} = \frac{(2/\pi) a_{0,2} a_{0,3} (\delta \sqrt{a_{0,2}^2 + a_{0,3}^2} + a_{0,2} \zeta \sqrt{1 + a_{0,2}^2})}{a_{0,3}^2 + a_{0,2} (a_{0,2} + a_{0,3}^2 + a_{0,2} a_{0,3}^2 + \sqrt{(1 + a_{0,2}^2)(a_{0,2}^2 + a_{0,3}^2)})}, \quad (6)$$

where $a_{0,2}$ and $a_{0,3}$ are the consumption rate of the sole consumer and of the sole predator, respectively, $\delta = r_{\beta 1} - r_{\beta 2} + r_{\alpha 2}$, and $\zeta = r_{\beta 1} - r_{\alpha 2} - r_{\beta 3} + r_{\alpha 3}$. Note that δ

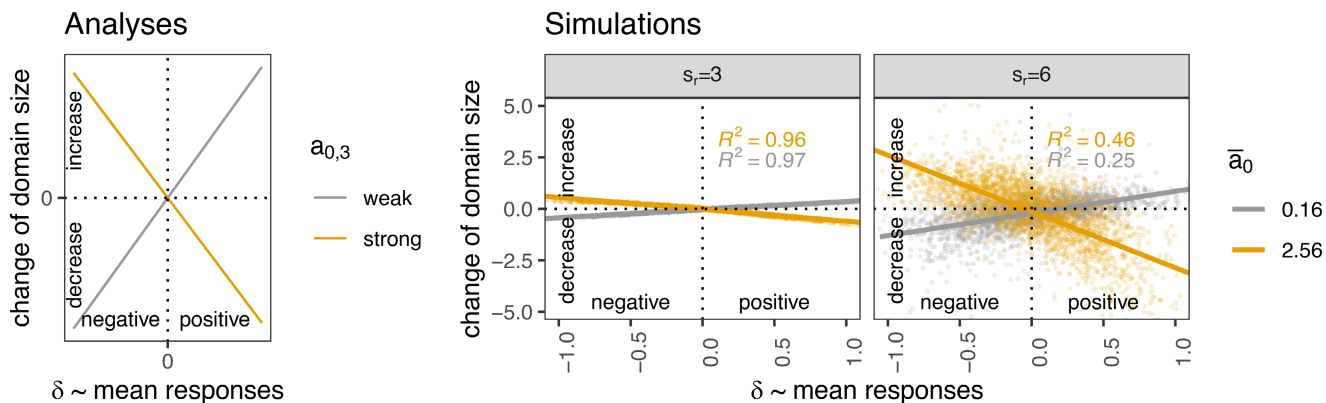


FIGURE 3 Mean species responses and the strength of consumption predict the effects of environmental change. The left panel shows the analytical results in communities with three species, where ‘weak’ and ‘strong’ refer to the consumption rate of species 3 without environmental change effects ($a_{0,3} < 1$ and $a_{0,3} > 1$ respectively). The right panel shows the simulation results for communities with s_r resource species and $s_r/3$ consumer species, where \bar{a}_0 is the mean consumption rate across consumers. In the analyses, the effect of an environmental change ϵ on the domain size Ξ is $d\Xi/d\epsilon$. In the simulations, this effect is the base-10 log ratio of Ξ with and without environmental change. Lines are linear trends to aid visualisation.

is essentially identical as in Equation (5): it sums responses of resources and consumers and averages those responses if there are multiple species per trophic level (not the case here). Importantly, while δ only depends on responses of resources and consumers, ζ depends on responses of all trophic levels. When the consumption rate is weak, δ suffices to predict the effects on coexistence. Conversely, when consumption is strong, predator responses also matter (contained in ζ) (Figure 4, left panel). Another conclusion is that the signs of δ and ζ fully determine whether environmental change will shrink or expand the feasibility domain. This happens because all the terms that contain $a_{0,2}$ and $a_{0,3}$ are positive. Thus, in contrast to bitrophic communities, the ecological characteristics (strength of consumption and predation) can only change the magnitude of the effect on coexistence, not its sign.

Finally, in very large bi- and tritrophic communities (Grilli et al., 2017, typically several dozens of species), we again find that effects on feasibility domain size are proportional to mean species responses (Data S1, Section 1.2.2):

$$\left. \frac{d\Xi}{d\epsilon} \right|_{\epsilon=0} \propto \bar{r}_{\beta r} - \bar{r}_{\beta c}, \quad (7)$$

where $\bar{r}_{\beta r}$ and $\bar{r}_{\beta c}$ are the mean responses of resource intrinsic growth and consumer mortality respectively. This expression holds for bi- and tritrophic communities alike, when the number of resource species is much larger than the number of predator species (which is typically the case). Note that this expression equals δ when setting $\bar{r}_{\alpha c} = 0$.

Simulations

We performed simulations to test if effects on coexistence in communities of intermediate size depend on

mean species responses, as found in the analyses. For a community of arbitrary size, we extend δ and ζ to arbitrary community size such that they retain their meaning from the three species case: $\delta = \bar{r}_{\beta r} - \bar{r}_{\beta c} + \bar{r}_{\alpha c}$, and $\zeta = \bar{r}_{\beta r} - \bar{r}_{\alpha c} - \bar{r}_{\beta p} + \bar{r}_{\alpha p}$, where $\bar{r}_{\beta r}$, $\bar{r}_{\beta c}$, $\bar{r}_{\alpha c}$, $\bar{r}_{\beta p}$ and $\bar{r}_{\alpha p}$ are the mean responses of resource intrinsic growth, consumer mortality, consumption by the consumers, predator mortality and consumption by the predators respectively.

Confirming the analytical results for the three-species case, δ and the mean consumption rate \bar{a} predict the effects on feasibility domain size in bitrophic communities of intermediate size (Figure 3, right panel). More specifically, and exactly as predicted by the three species results, when consumption rates are weak, environmental change types hampering population growth ($\delta < 0$) will shrink the feasibility domain. Environmental change types stimulating growth ($\delta > 0$) tend to make the feasibility domain larger. When consumption rates are strong, the opposite is true. Again, consumption rates below the rate that maximises the feasibility domain are ‘weak’, while those above that threshold are ‘strong’ (Figure S2). Also for the tritrophic case, our simulations confirm the analyses of the three species model: δ and ζ predict effects on feasibility domain size (Figure 4, right panel), where the latter (former) is more important when consumption is weaker (stronger). Again, as found for the three species community, the ecological characteristics of the community (mean consumption) only change the size, not the sign of the prediction.

Application to temperature change and pollution

Our theoretical results have implications for our understanding of how two important cases of environmental change can affect coexistence: temperature change and

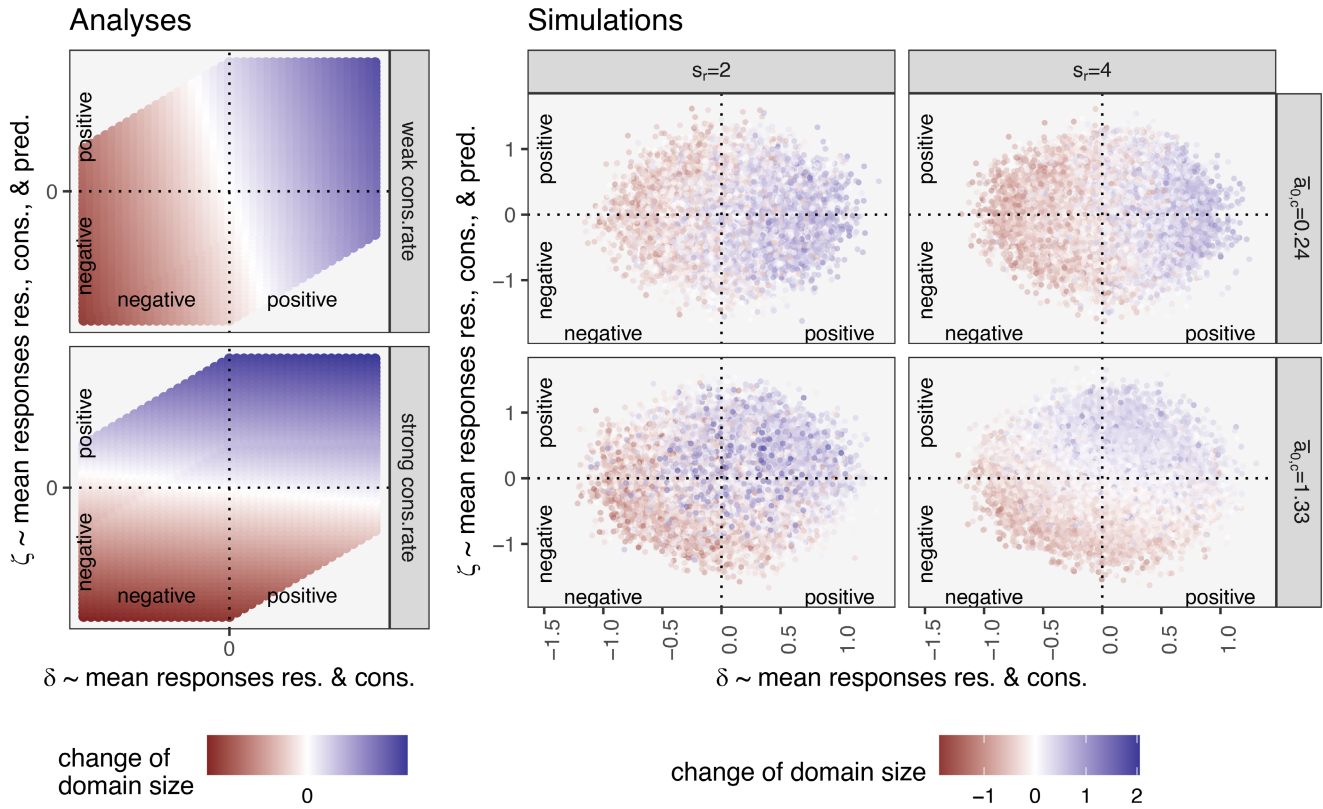


FIGURE 4 Mean species responses of resources and consumers, and of resources, consumers and predators predict effects of environmental change. The left panel shows the analytical results in communities with three species (one at each trophic level), where ‘cons. rate’ is consumption rate, and ‘res.’, ‘cons.’ and ‘pred.’ are resource, consumer and predator. The right panel shows the simulation results for communities with s_r resource species, a single consumer ($s_c = 1$) and a single predator (setting $s_c = 2$ yields qualitatively similar results, Figure S4). Depending on whether average consumption by the consumers ($\bar{a}_{0,c}$) is weak (top panels) or strong (bottom panels), δ (x axis) or ζ (y axis) is more important. In the analyses, the effect of an environmental change ϵ on the domain size Ξ is $d\Xi/d\epsilon$. In the simulations, this effect is the base-10 log ratio of Ξ with and without environmental change.

pollution. We focus on the case of a bi trophic community where consumption is weak.

Substituting the species responses to temperature (Data S1, Section 1.4) into $\delta = \bar{r}_{\beta r} - \bar{r}_{\beta c} + \bar{r}_{ac}$ yields:

$$\delta = \overline{\omega_r^{-2} (T_{\text{opt},r} - T_r)} + \overline{\omega_c^{-2} (T_{\text{opt},c} - T_r)} - T_r^{-2} k^{-1} \bar{E}_{A,c}, \quad (8)$$

where $T_{\text{opt},r}$ and $T_{\text{opt},c}$ represent the optimal temperatures of resources and consumers respectively. Similarly, ω_r and ω_c represent temperature niche width of the resources and consumers respectively. Further, T_r , k and $E_{A,c}$ are the reference temperature (i.e., the temperature prior to the temperature change), Boltzmann's constant and activation energy. The first two terms in Equation (8) represent responses of the resources' intrinsic growth and the consumers' consumption rate. The third term represents the response of the consumer's mortality rate, and can only be negative because $k > 0$ and $E_{A,c} > 0$. Equation (8) leads to the following conclusions. First, when the reference environmental temperature is on average already too high for both trophic levels ($\overline{T_{\text{opt},r} - T_r} < 0$ and $\overline{T_{\text{opt},c} - T_r} < 0$, and therefore $\delta < 0$), further warming inevitably shrinks

the feasibility domain. Second, warming increases the size of the feasibility domain in environments that are regarded as too cold for most species (i.e., when $\delta > 0$). Third, the effect of temperature on consumer mortality (higher temperature makes for faster mortality) always shrinks the feasibility domain.

Substituting the species responses to pollution (Data S1, Section 1.4) into $\delta = \bar{r}_{\beta r} - \bar{r}_{\beta c} + \bar{r}_{ac}$ yields

$$\delta = - \left(\overline{k_{\beta,r}^{-1}} + \overline{k_{\alpha,c}^{-1}} + (\beta_{\text{max}} - 1) \overline{k_{\beta,c}^{-1}} \right), \quad (9)$$

where $\overline{k_{\beta,r}^{-1}}$, $\overline{k_{\alpha,c}^{-1}}$, $\overline{k_{\beta,c}^{-1}}$ are the mean sensitivity of resource intrinsic growth, of consumption and of consumer mortality. This result shows that the effect of pollution on the size of the feasibility domain only depends on the sum of mean species sensitivities, quantified as the inverse k^{-1} of the inflection points, as is typically done (Ritz, 2010). Since $\beta_{\text{max}} \geq 1$ (it is the maximal fold increase of consumer mortality) and since the inflection points are all positive, Equation (9) further shows that pollution always results in $\delta < 0$: pollution will always shrink the feasibility domain, reducing the scope for coexistence.

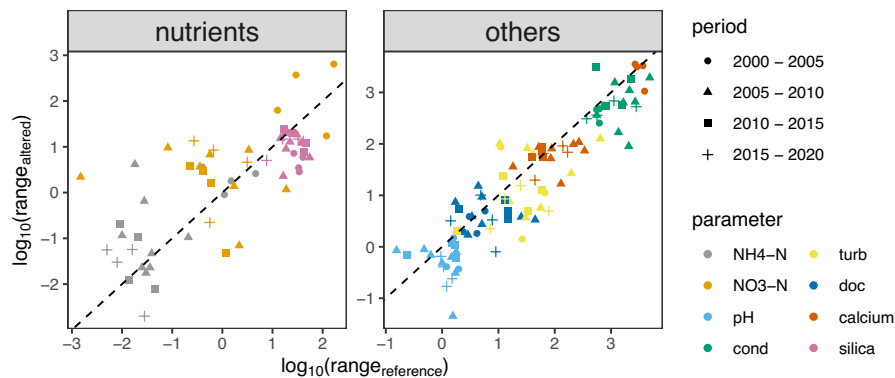


FIGURE 5 Human activity shrunk feasibility domains of empirical communities. The x axis shows the range of chemistry variables along which a community is found ('used' range) across reference sites, while the y axis shows that across altered sites. The shape of a point corresponds to sampling period, and the colour corresponds to water chemistry variable. We found that the altered sites have lower 'used range' in general. The dashed line is the identity line. The identified communities are listed in [Table S1](#); statistical results are in [Table S2](#).

Application to field data

Our proposed spatial interpretation of the feasibility domain size ([Figure 2](#)) assumes that dispersal and locally varying species interactions do not influence our capacity to predict effects on persistence across different sites from mean species responses. Simulations with a meta-community model show this is true. We find that, despite dispersal and locally varying consumption and predation, the same mean responses predict the effects of environmental change on persistence across sites, which are by design locally varying ([Figures S5 and S6](#)). Thus, we can apply our spatial interpretation of the theory to analyse our monitoring data.

Macroinvertebrate counts in streams across continental USA show that communities only persist across severely restricted ranges of environmental conditions (here, water chemistry variables). Indeed, the range of water chemistry variables in which a community persists is typically about one log-unit smaller than the available range of water chemistry variables ([Figure S7](#)). This suggests that these communities are not able to persist beyond their used ranges, confirming an assumption of our main analysis on environmental change effects on coexistence.

We found 15 communities that were observed across at least three reference sites (3–33 sites) and three altered sites (3–5 sites). These communities in most cases consisted of genera belonging to the family of *Chironomidae* ([Table S1](#)), which are known to tolerate poor water quality and are therefore to be found back across both reference and altered sites. While the number of sites that share a single community is admittedly low, our analysis indicates that communities covered less variable water chemistry across altered sites than across reference sites. Specifically, the *used range* is typically smaller across altered sites than across reference sites ([Figure 5](#)). Overall, this was the case for 104 out of the 160 combinations of community and

water chemistry parameter. When focusing on water chemistry variables that are not nutrients, the *used range* was smaller across altered sites for 72 out of the 100 combinations of community and water chemistry parameter. A statistical analysis confirms this result: The log ratio of the reference and altered used ranges was significantly positive for four of the six chemistry variables that were not macronutrients (pH, conductivity, turbidity and silica, [Table S2](#)), across all four periods. Period on itself did not affect this ratio. Taken together, and adhering to the spatial interpretation of the feasibility domain ([Figure 2](#)), this result would suggest that human activity shrunk the feasibility domain.

DISCUSSION

New insights

We have modelled environmental change as small changes of intrinsic growth and species interactions (consumption and predation) and evaluated the consequences for coexistence using the concept of feasibility. We find that means of species responses predict much of the effects of environmental change on coexistence. This is to some extent surprising, since species responses alone have been found incapable of predicting community-level effects because of species interactions (De Laender, 2018; Thomas et al., 2017; Zhang et al., 2017). Our results do not contradict these findings, for three reasons. First, we do not focus on the persistence of individual species or trophic levels, but instead, consider the persistence of the community as a whole. Second, the influence of species interactions is encoded in the sums of mean responses (δ and ζ). For example, an increase in consumers' mortality rates can be offset by an increase in resources' intrinsic growth, causing no net change in the size of the feasibility domain. Third, the average strength of consumption and

predation does influence the sign (bitrophic) and/or size of the effects on coexistence (bi- and tritrophic).

Many analyses of environmental change effects on consumer–resource communities consider cases where a single resource feeds a single consumer, as this is a fundamental building block of more complex models (Amarasekare, 2015; Synodinos et al., 2021; Turschwell et al., 2022; Uszko et al., 2017; Vinton & Vasseur, 2022). In most of these cases, positive consumer density guarantees the feasibility of the species pair, as the consumer cannot persist without the resource. For instance, the positive effects of temperature on consumption would increase consumer biomass without jeopardising the existence of the sole resource, which implies that any factor stimulating consumption will make the feasibility domain larger. Here, we consider the case where there are more resources than consumers. As explained in Data S1 (Section 3), the effect of the consumption rate on coexistence when there are more resources than consumers is unimodal. Since any multiplicative effect of environmental change is in essence equivalent to an effect on the consumption rate (Equation 4), said unimodality will make positive effects facilitate coexistence when consumption is weak, but hamper coexistence when consumption is strong, explaining the role of $h(a_{0,3})$ in Equation (5).

The fact that mean species responses predict effects on coexistence sheds new light on the consequences of thermal mismatches in consumer–resource modules. A thermal mismatch refers to trophic levels having different temperature optima and/or thermal niches (Dell et al., 2014). Analyses have shown that such a mismatch will affect community dynamics and realised thermal niches (Amarasekare, 2015; Vinton & Vasseur, 2022). Our results show that, when the size of the feasibility domain is the response variable, such a mismatch will not consistently hamper or promote coexistence. Rather, what matters is the total deviation of the thermal optima of the trophic levels from the reference temperature. Thus, a thermal mismatch can lead to exactly the same effect on coexistence as when temperature optima are identical for both trophic levels. It is well-established that variation among species responses to environmental change is important for how community composition and ecosystem function respond to environmental change (Elmqvist et al., 2003; Ross et al., 2023; Song et al., 2020). For example, more varied responses will cause greater indirect effects, which can either exacerbate or dampen the resulting net effects on equilibrium densities (Chu et al., 2016; Kleinhesselink & Adler, 2015). Similarly, more varied responses will reduce the fraction of species able to persist (Holmes et al., 2021). Here, we find that variation in response across species within trophic levels ceases to be important when considering the size of the feasibility domain. Only the mean response across species within a trophic level matters. This is because our focus is not on the persistence of a focal

species, but on how much one can perturb parameter values without losing *any* species. For instance, two feasibility domains of the same *size* may still have different *shapes*, making it harder for a specific species to survive a parameter change in the first than in the second domain. Considering the effects of environmental change on the geometry of the feasibility domain, as discussed elsewhere (Grilli et al., 2017; Tabi et al., 2020), is, therefore, a logical avenue for future work.

Limitations

Our analyses come with a number of limitations. First, we focus on small environmental changes. Thus, our results cannot be extrapolated to broad environmental gradients, along which we expect nonmonotonic community responses (De Laender et al., 2016; Spaak et al., 2017; Uszko et al., 2017). Second, we consider changes in the likelihood of species coexistence, and therefore our results tell nothing about the probability for species loss or system collapse, for which other formalisms are needed (Barbier et al., 2018; Zelnik et al., 2018). Third, we assume species interactions to be linear because of low computational cost and high analytical tractability. If and how including nonlinear interactions would affect our conclusions is hard to anticipate. For the limiting cases where species interactions are very weakly or very strongly nonlinear, results are unlikely to deviate much from the linear case (Grilli et al., 2017). Also in very small communities (\leq three species), more complex species interactions are not expected to overly affect the size of the feasibility domain (Saavedra et al., 2020). Nevertheless, future studies are needed to test the robustness of our results. Finally, directly observing the feasibility domain using field data is challenging beyond three species. We have therefore explored an alternative route, which has used site-to-site variation of environmental conditions as a proxy variable for the feasibility domain. While our data analysis does suggest that communities cover smaller ranges of environmental variables across altered (i.e., nonreference) sites, we were not able to rigorously test the assumptions the analysis depends on. In addition, despite the large amount of data, the number of sites in which a single community persisted was fairly small. A higher spatial resolution of community composition is needed to scrutinise our findings.

Implications and applications

The practical implications of our results depend on how to interpret changes in the feasibility domain size. Probabilistic interpretations (Saavedra et al., 2020) have explained why certain community compositions are found more often (Medeiros et al., 2020), and which compositions are more sensitive to environmental change (Tabi et al., 2020). Our interpretation is similar, as one

considers the community's feasibility domain size as the fraction of sites in which said community can persist. We show that this interpretation is robust to the inclusion of dispersal and site-to-site variation of species interactions. A smaller feasibility domain thus constrains the local environmental conditions a community can deal with. An intuitive expectation would therefore be that a negative effect on the feasibility domain of different communities would result in a greater spatial heterogeneity of community composition. If true, this explanation has a potentially important implication for field studies, as it could help explain the absence of consistent biotic homogenisation of community composition in some of these studies (Finderup Nielsen et al., 2019; Karp et al., 2012; Petsch et al., 2021). While their implications for beta diversity need to be evaluated in detail, our results make clear that detrimental effects on population growth do not automatically homogenise community composition. Instead, differentiation may ensue, as it gets harder for one single community to persist across many sites.

We have applied our theory to two relevant cases of environmental change: temperature change (Masson-Delmotte et al., 2021) and pollution (Bernhardt et al., 2017). These case studies show that one can predict effects on coexistence from average temperature optima and sensitivities to pollution. These results expand earlier findings for temperature effects on small consumer–resource modules (Amarasekare, 2015; Vasseur & McCann, 2005) to effects of any multiplicative environmental driver on bi- and tritrophic communities of arbitrary size. For many environmental drivers, effects on proxies of intrinsic growth (e.g., reproduction or mortality) of single species are contained in bioassay databases. Notable examples include pollutants (Scharmüller et al., 2020), temperature (Thomas et al., 2012) and nutrients (Edwards et al., 2015). In the limit of very large communities, we find that responses of intrinsic growth are most important. We, therefore, submit that the approach we present can capitalise on said data to inspire methods in conservation and environmental protection. Potential applications include the identification of drivers (or driver combinations) that are most likely to limit coexistence (De Laender, 2018; Orr et al., 2020; Thompson et al., 2018). One simple example resulting from our two case studies is that pollution and temperature change are two qualitatively different cases of environmental change, where the former will always shrink the feasibility domain, while the latter can both shrink and inflate the feasibility domain. Such findings contribute to a much-needed synthetic understanding of environmental change effects. Ecosystems increasingly face various kinds of environmental change (Birk et al., 2020). Being able to predict community and ecosystem responses is a prerequisite to effective conservation (Orr et al., 2020). To this end, analyses of field data often explore putative statistical relationships between environmental

drivers and various descriptors of biological communities. (Daskalova et al., 2020; Malaj et al., 2014; Outhwaite et al., 2020; Schulz et al., 2021). Our results suggest that combining such analyses with data on species responses is an avenue worth exploring.

AUTHOR CONTRIBUTIONS

FDL, GB, GM and CC designed the study. FDL performed analyses and simulations with help from GB, CC and CS. TC carried out the stability analysis. FDL performed field data analysis with help from SLR, MBM and MS. FDL wrote the manuscript and all authors contributed substantially to revisions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT


All code and data are downloadable from GitHub (https://github.com/fdelaend/De_Laender_et_al_feasibility) and on Dryad (<https://doi.org/10.5061/dryad.2280gb5xs>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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