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LETTER

Shifts of community composition and population density substantially affect ecosystem function despite invariant richness

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Abstract

There has been considerable focus on the impacts of environmental change on ecosystem function arising from changes in species richness. However, environmental change may affect ecosystem function without affecting richness, most notably by affecting population densities and community composition. Using a theoretical model, we find that, despite invariant richness, (1) small environmental effects may already lead to a collapse of function; (2) competitive strength may be a less important determinant of ecosystem function change than the selectivity of the environmental change driver and (3) effects on ecosystem function increase when effects on composition are larger. We also present a complementary statistical analysis of 13 data sets of phytoplankton and periphyton communities exposed to chemical stressors and show that effects on primary production under invariant richness ranged from −75% to +10%. We conclude that environmental protection goals relying on measures of richness could underestimate ecological impacts of environmental change.

Keywords

Algae, biodiversity, coexistence, community ecology, modelling, primary production.

Ecology Letters (2017) **20**: 1315–1324

INTRODUCTION

Many ecosystem assessments today use species loss as the prime ecological response to environmental change (Lenoir *et al.* 2008; Ehrlen & Morris 2015; Keith *et al.* 2015; Urban 2015). Urged by prognoses of a sixth mass extinction (Ceballos *et al.* 2015; Regnier *et al.* 2015; Urban 2015), biodiversity–ecosystem function research has examined how species loss maps to functional impairment in a variety of ecosystem types (Cardinale 2011; Mora *et al.* 2014; Tilman *et al.* 2014; Lefcheck *et al.* 2015). Despite this tacit assumption of richness as a primary driver of function, it is well known that environmental change can affect function in ways that do not involve changes in species richness (Loreau 1998; Fox 2006).

Effects on function at invariant richness can occur through effects (a) on species contributions to functions and (b) on community composition (Fox & Kerr 2012), here defined based on the species presence/absence, not on relative densities (Fig. 1). Case (a) occurs when population density (or biomass) and/or per-capita contributions to function are affected (the amount of function delivered per density unit) (Fox 2006; Suding *et al.* 2008). Case (b) occurs when the loss of a number of species coincides with the gain of the same number of species, with the gained species contributing more or less to function than the lost species. Effects of the environment on species contributions to function and on community composition may overshadow the effects of changes in richness (Larsen *et al.* 2005; Wardle *et al.* 2011). For example, Lohbeck *et al.* (2015) found that changes in biomass contributed more to changes of ecosystem processes than did changes in species richness during succession. Winfree *et al.* (2015) found that the density of pollinators had a stronger effect on pollination than did random and non-random changes of richness. In general, it is well known that environmental changes affect population density or biomass before it affects species loss (Gaston & Fuller 2008; Hillebrand *et al.* 2008; Hull *et al.* 2015), which raises the question to what extent such effects can change ecosystem function under situations where species richness remains constant.

Theoretically exploring to what extent environmental change may affect function without affecting richness requires

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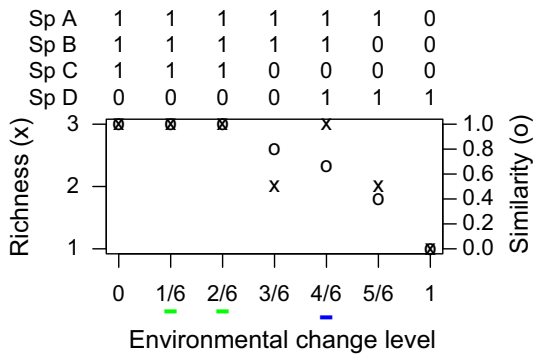*Correspondence: E-mail: juerg.spaak@unamur.be*

Figure 1 Richness and community composition change along a hypothetical gradient of environmental change, from 0 (no change) to 1 (maximum change). Similarity with the composition at no change quantifies compositional shifts. The top panel corresponds to the presence (1)/absence (0) matrix of the four species at seven levels of change. At green levels, both richness and composition are unaffected (case *a* in the introduction). At the blue level, richness is unaffected while composition is (case *b* in the introduction).

considering the covariance between the contribution of a species to function, i.e. its density and its per-capita contribution (Suding *et al.* 2008), and its negative or positive response to environmental change (Larsen *et al.* 2005; Li *et al.* 2009; Püttker *et al.* 2015; Radchuk *et al.* 2016). For example, when species contributing most to function are least affected, environmental change drivers that elicit negative responses will affect function less than when species contributing most to function are affected most. However, in the absence of environmental fluctuations, species with low population densities are more extinction prone when they suffer disproportionately in terms of competitive strength compared to high density species (Chesson 2000). Thus, coexistence requirements constrain interspecific differences in environmental effects, and therefore, the amount of function that can theoretically be lost without resulting in species loss. Formal mathematical analysis is therefore needed to integrate correlations between environmental effects and species contributions to function, and coexistence requirements. We are unaware of such an analysis in the literature.

Empirical observations of effects on function that are not accompanied by effects on richness can require multiple levels of environmental change to be tested along a broad gradient. This is because the probability of finding a level of environmental change that affects function but not richness increases both with the number of distinct levels of environmental change and the breadth of the gradient tested. However, empirical studies typically test only the effects of a small number of environmental change levels across a restricted gradient (Hautier *et al.* 2015; De Laender *et al.* 2016), which makes it difficult to detect effects on function in the absence of effects on richness. Alternative approaches that infer function and richness beyond tested levels of environmental change are therefore needed. To achieve this, one needs to regress richness and function against environmental change level to gain statistical estimates of richness and function at levels not tested in the experiment (Ritz 2010).

Here, we evaluate the importance of effects of environmental change on ecosystem function in the absence of effects on

richness by adopting two approaches. First, we carry out a formal mathematical analysis on a community model (Eklof & Ebenman 2006). We focus on competitive communities, as this facilitates embedment within the bulk of the available empirical and theoretical literature (Cardinale *et al.* 2011; Tilman *et al.* 2014). We consider two cases of invariant richness: we either maintain invariant community composition, or require composition to change (Fig. 1). We do so for various covariances between the per-capita contributions to function, competitive strength and environmental effects on competitive strength. Our analysis represents two types of environmental change drivers: variables that decrease competitive strength (e.g. sub- or supraoptimal temperature, toxic chemicals) or increase competitive strength (e.g. resource enrichment) (De Laender *et al.* 2016). A second approach applies dose–response analysis to data from the literature. These data were drawn from microcosm experiments containing phytoplankton and periphyton exposed to chemical stressors, which constitute significant but understudied environmental change drivers (Malaj *et al.* 2014; Bernhardt *et al.* 2017). We discuss the implications of our results for theoretical and applied ecology.

METHODS

Model description and calculation of ecosystem function

We considered a community of *n* interacting species exposed to one environmental change driver. We used a Lotka–Volterra formulation so that sufficiently large environmental effects e_i (ranging between -1 and 1) on certain growth rates μ_i would result in the exclusion of the corresponding species and thus in effects on richness:

$$\frac{dN_i}{dt} \cdot \frac{1}{N_i} = \mu_i \cdot (1 - e_i) + \sum_{j=i}^{n} \alpha_{i,j} \cdot N_j \qquad (1)$$

N_i is the population density of species *i* and $\alpha_{i,j}$ are coefficients of intra- and interspecific interaction strength. All variables and their definitions are given in Table 1. Appendix S1 of the supporting information gives an extended version of Table 1, including all variables and definitions used in the supporting information. To make analytical handling feasible, we assume that all per-capita interspecific interactions are identical, i.e. $a_{i,j} = \alpha$ (for $i \neq j$, all species have equal effects on each other) and less negative than $a_{i,i} = -1$ to allow coexistence in the absence of environmental change. From this assumption, it follows that the growth rate μ_i is a proxy for competitive strength, and that the equilibrium density of species *i*, N_i^*, equals:

$$N_i^* = \frac{1}{1 + \alpha} \left(\mu_i - \frac{-\alpha n}{1 - \alpha(n-1)} \bar{\mu} \right) \qquad (2)$$

where $\bar{\mu}$ is the average of all competitive strengths μ_i (Appendix S2). In Appendix S3, we show that this equilibrium is the only stable point. The factor $\frac{-\alpha n}{1 - \alpha(n-1)}$ represents the effective competition each species experiences, which we will refer to as C_α^n in the rest of the text. In Appendix S4, we illustrate that C_α^n varies between 0 and 1.

Table 1 List of mathematical symbols used in the text

N_i, N_i^*	Density and equilibrium density of species i
$a_{i,j}$	Interaction coefficient between species i and j
μ_i, f_i, e_i	Growth rate (a proxy for competitive strength in our model), per-capita contribution to function, and environmental effects for species i
C_α^n	Effective competition
n	Number of species
EF_u, EF_c	Ecosystem function at the <u>u</u>nchanged and the <u>c</u>hanged site
ΔEF	Difference in ecosystem function between an unchanged and changed site
p	Proportion of species belonging to both sites
$EF_u^{(b)}$, $EF_u^{(u)}$	Ecosystem function at an unchanged site containing n species of type b and u respectively
$EF_c^{(b)}$, $EF_c^{(c)}$	As $EF_u^{(b)}$, $EF_u^{(u)}$, but for the changed site
$\Delta EF^{(b)}$	Difference in ecosystem function between two sites consisting of n species of type b
$\Delta EF^{(u,c)}$	Difference in ecosystem function between two sites. The unchanged site consists of n species of type u; the changed site consists of n species of type c

To link population densities to ecosystem function in an unchanged site EF_u, we introduce f_i as the per-capita contribution of species i to function:

$$EF_u = \sum_{i=1}^{n} f_i N_i^* = \frac{1}{1+\alpha} \sum_{i=1}^{n} f_i(\mu_i - C_\alpha^n \bar{\mu})$$

$$= \frac{n}{1+\alpha} \left(\bar{f}\bar{\mu} - C_\alpha^n \bar{f}\bar{\mu} \right) = \frac{n\bar{f}\bar{\mu}}{1+\alpha} \left(\text{cov}(f_r, \mu_r) + 1 - C_\alpha^n \right) \quad (3)$$

Here, $\text{cov}(f_r, \mu_r)$ is the covariance across species between their relative per-capita contribution $f_r = \frac{f}{\bar{f}}$ and their relative competitive strength $\mu_r = \frac{\mu}{\langle\bar{\mu}\rangle}$. A positive value for this covariance means that competitively dominant species contribute more to function than competitively inferior species, which increases total ecosystem function EF_u. In the results section, we derive the relative difference in ecosystem function in a site subject to environmental change (EF_c) and the unchanged site (EF_u) for two cases of invariant species richness: community composition is either identical between the changed and unchanged site (e.g. as is the case at the green levels in Fig. 1), or different (e.g. at the blue level in Fig. 1). Next, we quantify this difference using numerical calculations. We do so for two types of environmental change drivers: those that decrease competitive strength (i.e. where $e > 0$ for all species) and those that increase competitive strength (i.e. where $e < 0$ for all species).

Empirical relationships between environmental change, richness, and function

We collected data from micro- and mesocosm studies that tested for effects of chemical stressors, representing one of the two types of environmental change, on richness and function ($e > 0$). To this end, we searched the literature for studies that reported effects of chemical stressors on phytoplankton or periphyton richness and biomass production. The data sets we found represent a broad range of systems, including indoor

microcosms of several litres to large outdoor artificial ditches, and contained between 7 and 31 taxa in the absence of chemical stress. The chemical stressors used were mostly herbicides (four data sets for linuron, one for a herbicide mixture containing atrazine and one for diuron). Other stressors were copper, the fungicide triphenyltin acetate, and salt. For six data sets (8–13 in Table S2), only periphyton or phytoplankton communities were present in the experimental units. In the other seven data sets, also zooplankton and macroinvertebrates were present. All details on our literature search and data processing are available in Appendix S5.

For each data set, we regressed species or genus richness and primary production (chlorophyll *a* or biovolume of the considered periphyton or phytoplankton community) against the stress level using generalised additive modelling (Wood 2006) (R package *mgcv*) with a smoothing spline and gamma link function, because richness and production were strictly positive numbers. We chose splines to allow a variety of relationships between chemical stress and diversity as well as primary production, ranging from monotonous to multimodal, and from positive to negative, without any constraint imposed by model structure. Based on visual inspection of model fits, we set the maximum number of knots to 4 to prevent overfitting. The response variable was either richness or primary production, and the predictor was the log-transformed chemical concentration. Log-transformation of chemical concentrations was done because exposure concentrations in the studies were not linearly spaced. We attributed half of the lowest non-zero concentration to the control to avoid log-transformation of zero. We repeated our analyses, replacing zero concentrations by one tenth and one-fifth of the lowest non-zero concentration, but this did not change our results (Appendix S5).

For data sets 1–7, we had community composition data so we could test if effects on function at invariant richness were accompanied by effects on composition. To do this, we regressed community dissimilarity with the control against the stress level in exactly the same way as for richness and primary production. We calculated Bray–Curtis dissimilarity relative to the control with the functions *vegdist* and *decostand* from the R package *vegan* 2.4.0 (Oksanen *et al.* 2016; R_Core_Team 2016). We first converted species abundances to the presence/absence data such that the dissimilarity values were only based on compositional and not on structural differences, in line with the definition of community composition we used in the theoretical analysis.

Based on the fitted relationships, we predicted the response Y (Steudel *et al.* 2012) of richness, primary production, and similarity with the control (for studies 1–7 only) to 1000 evenly spaced log-transformed chemical stress levels, varying between the lowest and highest log-transformed chemical stress level: $Y = \frac{X_t - X_0}{X_0}$

where X_t and X_0 are the predicted values (richness, primary production, similarity with the control) at treatment t and the control respectively. We calculated upper and lower limits around Y by setting X_t to the upper (mean prediction plus two standard errors) and lower (mean prediction minus two standard errors) limit of the confidence interval of the variable of interest (richness, production, similarity) respectively. For

X_0, we always took the mean prediction. To estimate the effect on function or similarity at invariant richness, we tested at which stress levels the upper and lower limits of Y for richness included zero. At these stress levels, we inspected the upper and lower limits of Y for function (all studies) and similarity (studies 1–7 only). These values represent primary production and similarity values estimated from the data, for stress levels at which the statistical relationships did not suggest effects on richness.

RESULTS

Model analysis for invariant community composition

When the same species are present in the changed and unchanged site, the relative difference in ecosystem function between the two sites is (see Appendix S6a):

$$\frac{\Delta EF}{EF_u} = -\bar{e}(1 + \text{cov}(e_r, \mu_r))\left(1 + \frac{\text{cov}(f_r, (\mu e)_r) - \text{cov}(f_r, \mu_r)}{\text{cov}(f_r, \mu_r) + 1 - C_\alpha^n}\right) \quad (4)$$

where ΔEF is the difference in ecosystem function between the changed and unchanged site ($\Delta EF = EF_c - EF_u$), μe is the difference in competitive strength between both sites, and the other symbols are as in eqn 3. Overbars denote community-level averages; subscripts r denote relative quantities, i.e. quantities divided by their average value (see Methods). Eqn 4 shows that $\frac{\Delta EF}{EF_u}$ does not depend on average competitive strength or the average per-capita contribution to function.

$\frac{\Delta EF}{EF_u}$ is the product of three factors. The first factor ($-\bar{e}$) indicates that $\frac{\Delta EF}{EF_u}$ is proportional to the community average environmental effect $\bar{e}$. It reflects the negative or positive effects on function caused by environmental change drivers that increase ($\bar{e} < 0$, see eqn 1) or reduce ($\bar{e} < 0$) competitive strength.

The second factor $(1 + \text{cov}(e_r, \mu_r))$ quantifies the influence of the covariance between the relative competitive strength and the relative environmental effect on $\frac{\Delta EF}{EF_u}$. If the best competitors are affected most (i.e. $\text{cov}(e_r, \mu_r) > 0$), the difference in EF is larger than when the worst competitors are affected most. This factor highlights a main result: the amount of function lost or gained at invariant richness can in theory be arbitrarily large, even when the average effect $\bar{e}$ (given by the first factor) is small. This is because the upper limit of $\text{cov}(e_r, \mu_r)$, and therefore, of the second factor of eqn 4, can in theory be arbitrarily large.

The third factor $\left(1 + \frac{\text{cov}(f_r, (\mu e)_r) - \text{cov}(f_r, \mu_r)}{\text{cov}(f_r, \mu_r) + 1 - C_\alpha^n}\right)$ combines three different elements: (1) the covariance between relative loss or gain of competitive strength $(\mu e)_r$ and relative per-capita contribution to function (f_r), (2) the covariance between relative competitive strength in the unchanged site (μ_r) and relative per-capita contribution to function and (3) the effective competition C_α^n (see Methods). This factor highlights another main result: effective competition, which is constrained between 0 and 1 (Appendix S4), will often have a smaller impact on ecosystem function change than the covariances between competitive strength, environmental effect, and per-capita contribution to function. These covariances can even cause

environmental change drivers that decrease (increase) growth to increase (decrease) function, contrary to intuition. This is most easily understood for the case where effective competition is near its maximum ($C_\alpha^n \approx 1$). In that case, the third factor of eqn 4 simplifies to $\frac{\text{cov}(f_r, (\mu e)_r)}{\text{cov}(f_r, \mu_r)}$ such that the sign of that factor is positive when both covariances share the same sign or negative if not.

The exact size of the relative difference in ecosystem function (eqn 4) depends on the values chosen for μ, e, and f. While f can be chosen freely, the values for μ and e cannot, as coexistence of all species in both sites is required (Appendix S7). To calculate the exact size of the relative effect on EF at invariant richness and community composition, we randomly generated $2 \cdot 100\,000$ communities and calculated their $\frac{\Delta EF}{EF_u}$ values using eqn 4. For the first 100 000 communities, we considered environmental change drivers that stimulated competitive strength $\bar{e} \sim u[-0.5, 0]$. For the other 100 000 communities, we chose $\bar{e} \sim u[0, 0.5]$. For both sets of communities, we sampled across a broad range of weak to strong per-capita interaction strengths ($\alpha \sim u[-0.95, -0.05]$). Details on μ_i, f_i, e_i, n are given in Appendix S8a.

Our calculations show that, for the range of environmental effects e selected here, the relative difference in EF ($\frac{\Delta EF}{EF_u}$) mostly had the opposite sign of $\bar{e}$ (as expected from the first factor of eqn 4). When strong competitors with high per-capita contributions to function were also affected most by environmental change ($\text{cov}(|e_r|, f_r) = 1$ and $\text{cov}(|e_r|, \mu_r) = 1$), this difference ranged from -60% to $+90\%$ (Fig. 2). Confirming eqn 4, environmental change drivers with positive (negative) effects on competitive strength can only cause negative
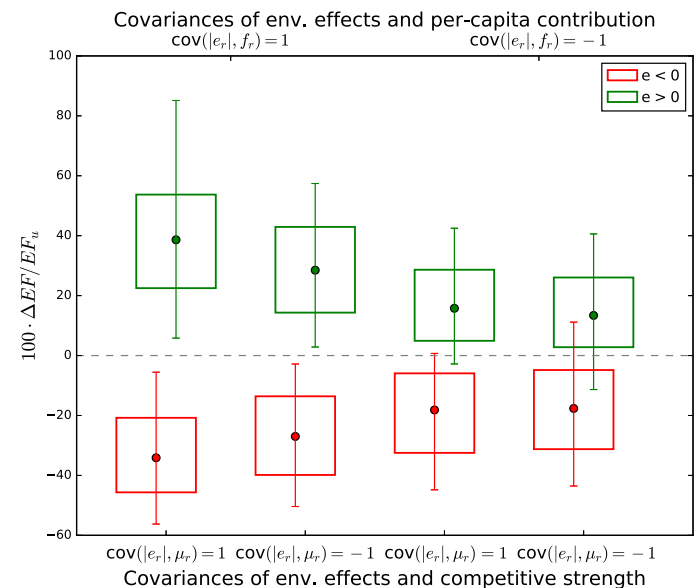

Figure 2 Effects on ecosystem function ($100 \cdot \frac{\Delta EF}{EF_u}$) at invariant richness and invariant community composition for environmental change drivers that decrease ($e > 0$) or increase ($e < 0$) competitive strength. Shown are median (dot), 25 and 75 percentiles (box), 5 and 95 percentiles (whiskers). Boxes are grouped by covariances ('cov') between the absolute value of relative environmental effect $|e_r|$, the relative per-capita contribution f_r, and the relative competitive strength μ_r.

(positive) effects on function when the covariance between the environmental effect and per-capita contribution to function is negative ($\text{cov}(|e_r|, f_r) = -1$, Fig. 2).

We performed additional calculations, relaxing our assumption that species contribution to function are linearly related to species density (see Methods). In Appendix S9, we show that asymptotic relations between species density and contributions to function decrease effects on ecosystem function.

Model analysis for variant community composition

When composition changes in a way that the number of species lost equals the number of species gained, there is no net change in species richness. To calculate the resulting relative change in ecosystem function, ΔEF, we introduce three species types: b species are common to b̲o̲t̲h̲ sites; u species are only present in the u̲n̲changed site and c species are only present in the c̲hanged site. We further assume that all species types have the same average per-capita contribution to function ($\bar{f}$). In Appendix S10, we show that relaxing this assumption leads to more complex mathematics but does not affect our results.

Let n be the total number of species in a site (by definition equal for both the unchanged and changed site) and p the proportion of species of type b. Then, we can write $\frac{\Delta EF}{EF_u}$ in a similar way as eqn 4 (Appendix S6b and c):

$$\frac{\Delta EF}{EF_u} = \frac{\Delta EF^{(b)}}{EF_u^{(b)}} \cdot \frac{pEF_u^{(b)}}{pEF_u^{(b)} + (1-p)EF_u^{(u)}} + \frac{\Delta EF^{(u,c)}}{EF_u^{(u)}} \cdot \frac{(1-p)EF_u^{(u)}}{pEF_u^{(b)} + (1-p)EF_u^{(u)}} \tag{5}$$

where $\Delta EF^{(b)} = EF_c^{(b)} - EF_u^{(b)}$ is the difference in ecosystem function between the changed (subscript 'c') and unchanged site (subscript 'u') if they would both contain the same n species (all of type b, hence both carry superscript '(b)'). Similarly, $\Delta EF^{(u,c)} = EF_c^{(c)} - EF_u^{(u)}$ is the difference in ecosystem function between the unchanged and changed site if they would not share a single species, i.e. contain n species of type u and n species of type c respectively.

Eqn 5 weighs the importance of compositional changes for $\frac{\Delta EF}{EF_u}$. It is a weighed sum of the relative difference in EF when there is either no ($\frac{\Delta EF^{(b)}}{EF_u^{(b)}}$) or total ($\frac{\Delta EF^{(u,c)}}{EF_u^{(u)}}$) compositional change. When p approaches 1 (more species shared by both sites), the second term of eqn 5 becomes less important and eqn 5 collapses to eqn 4. As p decreases, the importance of compositional change for $\frac{\Delta EF}{EF_u}$ increases.

Eqn 5 leads to another main result: Stronger compositional changes lead to lower $\frac{\Delta EF}{EF_u}$. This is because species of type c are by definition competitively inferior (have a lower μ) to species of type u (Appendix S7), which makes $EF_u^{(c)} < EF_u^{(u)}$ and $EF_c^{(c)} < EF_c^{(u)}$, and therefore, $\frac{\Delta EF^{(u,c)}}{EF_u^{(u)}} < \frac{\Delta EF^{(u)}}{EF_u^{(u)}} + \frac{EF_c^{(u)} - EF_u^{(u)}}{EF_u^{(u)}}$.

We randomly generated $10 \cdot 100,000$ communities (i.e. five different values for p at $e > 0$ and $e < 0$) that fulfilled coexistence criteria at both sites (Appendix S8b) and calculated $\frac{\Delta EF}{EF_u}$. These calculations confirm our main result: $\frac{\Delta EF}{EF_u}$ decreases as compositional change is more pronounced (down to -70%, Fig. 3).
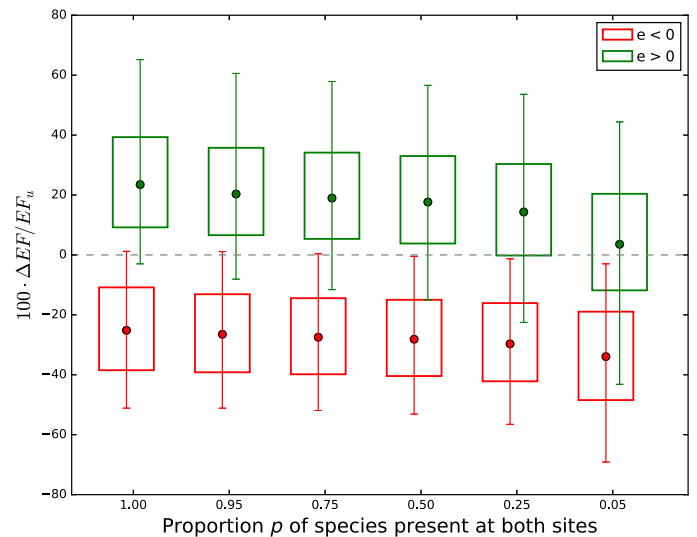

Figure 3 Effects on ecosystem function ($100 \cdot \frac{\Delta EF}{EF_u}$) for different fractions p of species that are present in both sites. Shown are median (dot), 25 and 75 percentiles (box), 5 and 95 percentiles (whiskers). Note that $p = 1.00$ corresponds to the case where both sites have identical community composition. $\frac{\Delta EF}{EF_u}$ becomes more negative as p is lower.

Empirical relationships between environmental change, richness and function

In most studies, stress (the type of change considered in our empirical analysis) reduced both richness (Fig. 4a) and function (Fig. 4b) of phytoplankton or periphyton communities. Stress increased richness and function in two and three cases respectively. Although studies varied in the size of the experimental unit and the presence of other communities, our data did not allow us to test robustly if these two factors influenced the response of phytoplankton or periphyton richness and function to stress.

Overall, effects on function were more pronounced than effects on richness. Importantly, effects on function occurred at lower stress levels than effects on richness. This led to effects on function at invariant richness in 9 out of the 13 data sets. The averages of these effects varied from -75% to $+10\%$.

Similarity among replicate control communities ranged between 55 and 94%. Treated communities became less similar to the control communities as stress intensified, but this effect was relatively small: the similarity of treated communities to the control communities was still between 28 and 91%. Effects on similarity at invariant richness were therefore also mostly small (absolute of average values always below 20%; Fig. 4c). Thus, our empirical results indicate that the effects on function at invariant richness (Fig. 4d) generally did not coincide with pronounced changes in community composition (Fig. 4e).

DISCUSSION

We found theoretical and empirical support for effects of environmental change on ecosystem function in the absence of
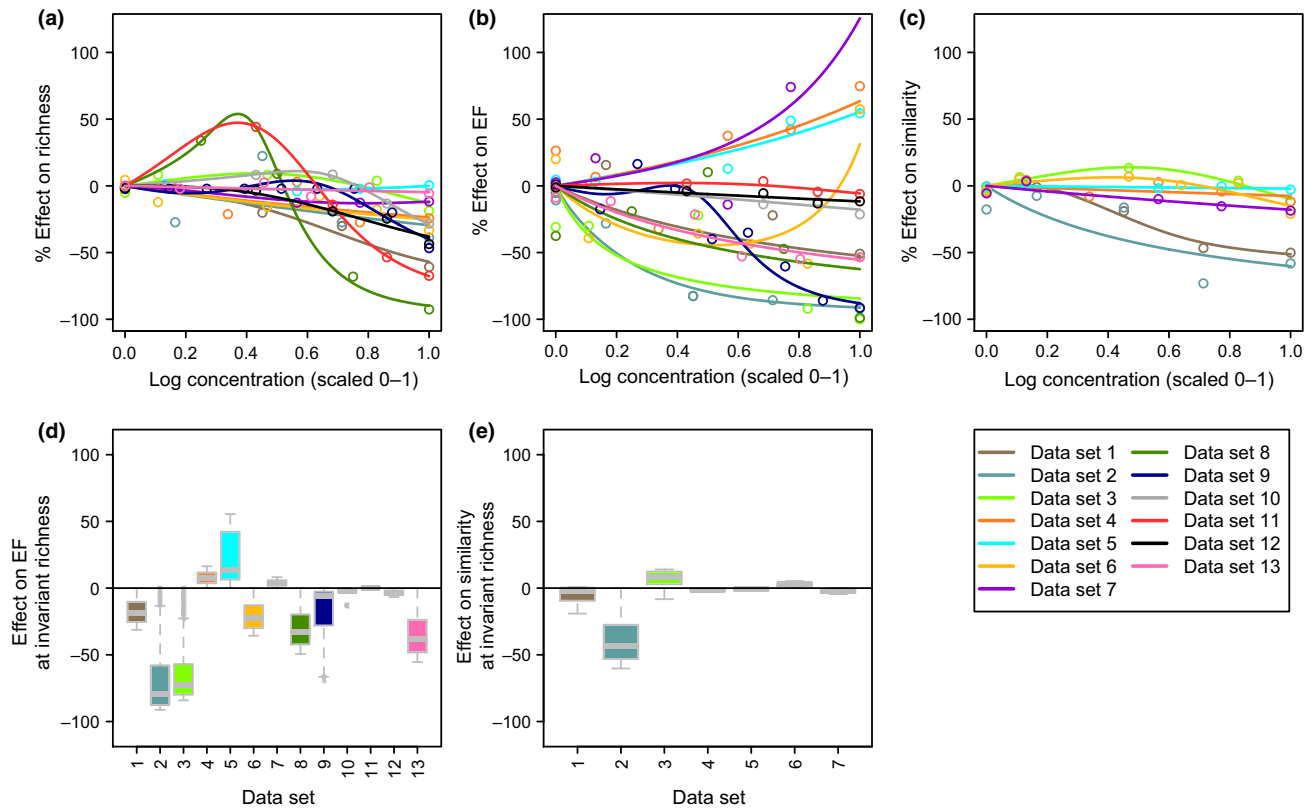
Figure 4 Effects of chemical stressors on richness (a), ecosystem function (EF, primary production), (b), and similarity with the average control composition (c) as observed in micro- and mesocosm studies. Symbols are data and lines are statistical models fitted to the data. Effects on EF (d) and similarity with the average control composition (e) at invariant richness, as estimated from the statistical models. Only for data sets 1–7 data on community composition were available.

effects on richness. Our theoretical analysis led to three important insights. First, small average environmental effects (taken across all species) may lead to a collapse of ecosystem function at invariant richness in competitive communities. Second, competitive strength, although pivotal for ecosystem function itself (Tilman *et al*. 2014), may be a less important determinant of relative ecosystem function change than the selectivity of the environmental change driver. This is because selectivity may cause per-capita contribution to function (*f*) to covary not only with the experienced environmental effect (or 'sensitivity', *e*), as included in response-effect trait frameworks (Suding *et al*. 2008), but also with competitive strength (μ). Third, relative effects on function are more negative as community composition is affected more. Our analysis of thirteen empirical data sets shows that phytoplankton and periphyton communities may produce up to 75% less (or 10% more) chlorophyll *a* or biovolume when exposed to stress levels that are not expected to affect richness (number of species or genera).

The two approaches we present address a common question in a complementary way, but it is unlikely that the patterns observed through statistical analysis are exclusively driven by the mechanisms included in the model. Our theoretical analysis considers an idealised minimal representation of a community competing for limiting resources at one trophic level. Our empirical analysis uses data sets of real phytoplankton and periphyton communities, seven of which (1–7) were embedded in a complex food-web containing macroinvertebrates and zooplankton. Phytoplankton and periphyton in these seven data sets were therefore potentially subject to trophic interactions that were external to the model. However, the response of phytoplankton and periphyton richness and function in these seven studies (Figs 4a and b) was most likely a direct consequence of the stress treatment and not of indirect effects caused by effects at other trophic levels. This is particularly the case for data sets 1–6, where the chemical stressors were all photosystem inhibitors and therefore targeted primary producers at the tested concentrations. In addition, in none of these six studies did any of the authors find evidence of direct treatment effects on the grazer communities, except in study 6, where rotifers were gradually replaced by cladocerans and copepods as stress levels increased (Cuppen *et al*. 1997). For data set 7, a profound treatment effect on grazers was reported (Roessink *et al*. 2006). This effect reflects at least partly a direct effect of the chemical stressor, the fungicide triphenyltin acetate, which is highly toxic to a wide range of aquatic organisms (Fargašová 1997). This reduction in grazing pressure likely contributed to the strong increase in chlorophyll a levels with increasing stress level observed (purple line in Fig. 4b).

Both analyses quantify the importance of density and community composition for ecosystem function differences along

environmental change gradients, as they deliberately focus on the case of constant richness. The decline of population densities and the role of density in sustaining functions have long been described qualitatively (Gaston & Fuller 2008). A recent meta-analysis of 114 paired control–treatment comparisons for various stressor types has shown that species richness of terrestrial animals responded less to stress than population density (Supp & Ernest 2014). Another recent global meta-analysis has shown that local compositional changes through time are commonplace (Dornelas *et al.* 2014). Our calculations show that, for the theoretical case of communities where negative interactions prevail, changes in community composition cause greater effects on function than when only population densities are affected. This difference can be explained by different competitive strengths, as explained in the results section.

We cannot be certain that our theoretical analyses, which are based on a model with no immigration, capture the temporal patterns observed in field data that almost certainly have been influenced by immigration (Dornelas *et al.* 2014; McGill *et al.* 2015). The compositional changes resulting from our model analysis should be interpreted as occurrences along a spatial environmental change gradient, not as temporal changes. More precisely, our model analysis can be thought of as representing a region composed of multiple isolated sites that initially had identical community compositions but have undergone different continuous levels of environmental change. This type of analysis can only approximate temporal changes within a site if historical contingency plays a minor role in community assembly (Fukami 2015). Else, models that account for the spatial embedment of communities need to be analysed (Fukami & Nakajima 2011).

We obtained an analytical derivation of the difference in ecosystem function between a site exposed to some type of environmental change and an unchanged site. This approach facilitates comparisons among types of environmental change, as we have shown by treating two different kinds of change, and among different community types. In this paper, we focused on competitive communities. However, if the conditions for coexistence can be defined for communities governed by other interaction types, our approach could be used to estimate the effects on function at invariant richness in various other community types.

Our analytical derivation also facilitates linking various types of (diversity and other) effects on function to mechanisms of species interaction and coexistence. In fact, the expression for ΔEF in the absence of effects on community composition or richness (eqn 4) is conceptually comparable to Fox & Kerr's (2012) context dependence effect on ecosystem function, using parameters that connect more directly to ecological mechanisms. Future theoretical studies could broaden the scope to cases where richness is allowed to change and as such link the statistical effects quantified by Price equation partitions (Fox 2006; Fox & Harpole 2008; Fox & Kerr 2012) to ecological parameters and variables. Linking community dynamics to partitioning techniques would allow theoretically exploring the relative contribution of density and composition to changes in function, both in the absence and presence of species loss.

Our model analysis is based on a number of assumptions. First, environmental change does not affect per-capita function f_i. Such effects do occur in reality, such as through physiological responses, and are often observed at environmental change levels that are lower than those affecting population densities (Miner *et al.* 2005; Schimel *et al.* 2007; Collins & Gardner 2009; Smith *et al.* 2009; Hawlena & Schmitz 2010; Pomati & Nizzetto 2013; Mensens *et al.* 2017). The omission of such effects thus means that our theoretical analysis most likely underestimates the effects on function at invariant richness.

Second, loss of genetic diversity within species because of environmental change (Sax & Gaines 2003) constitutes another mechanism that was not included in our model and that can also aggravate loss of function (Crutsinger *et al.* 2006; Hughes *et al.* 2008). Although gains of genetic diversity through environmental change have been described as well (Doi *et al.* 2010), genetic erosion is probably more likely for the case of chemical stressors considered in our analysis of empirical data (Barata *et al.* 2002; Ribeiro *et al.* 2012).

Third, we assume that environmental change does not change the strength of per-capita species interactions. Depending on the study system and environmental change driver, this assumption can be valid or not, and much work remains on how environmental change affects species interactions and coexistence (Hart & Marshall 2013; Barton & Ives 2014; Baert *et al.* 2016). The stress-gradient hypothesis postulates that, as stress intensifies, the sign of species interactions would shift from negative to positive, thus reducing the adverse effects of stress on richness and ecosystem function (Bertness & Callaway 1994). Our calculations do not represent such cases, and it is uncertain how including stress effects on per-capita interaction strength would influence our results.

Fourth, we implicitly focus on competitive communities for the reasons mentioned in the introduction and allow only symmetrical interactions. Thus, our analysis cannot be extrapolated to more complex community types such as food-webs. Considering complex networks of trophic interactions in the current paper would have impeded analytical solutions, but is a crucial next step to understand how environmental change drivers cause direct and indirect effects in food-webs (Sarmento *et al.* 2010; Brose *et al.* 2012; Kulkarni & De Laender 2017).

Fifth, our model is fully deterministic and therefore does not account for the higher risk of stochastic extinctions as population densities become smaller (Hubbell 2001). Because this risk will cause a more pronounced effect of environmental change on richness, it would make coexistence requirements more stringent, and thus reduce the effect on function at invariant richness.

Our finding that no loss of species can nevertheless lead to substantial shifts of function has important implications for both basic and applied ecology. More precisely, the outcome of the current debate on the scale of species loss (Vellend *et al.* 2013, 2017; Dornelas *et al.* 2014; Elahi *et al.* 2015; Newbold *et al.* 2015; Gonzalez *et al.* 2016) is probably more useful for biodiversity conservation and not that much for the conservation of ecosystem functions and services. Indeed, it is

highly possible that many of the ecosystems today that have lost species through some form of environmental change (Vitousek *et al.* 1997) were already suffering from functional loss before species loss occurred, as a consequence of other mechanisms, including changes in density (Hull *et al.* 2015; Winfree *et al.* 2015) and community composition (Pereira *et al.* 2010; Dornelas *et al.* 2014). This highlights an urgent need for regulatory monitoring and assessment to move beyond assessments based on richness. Even though effects on species richness can play a key role as an intermediary between environmental change and effects on ecosystem functions (Isbell *et al.* 2013; Hautier *et al.* 2015), our findings provide a theoretical and empirical demonstration that 'signals of constant richness should not lead to complacency' (McGill *et al.* 2015).

ACKNOWLEDGEMENTS

AUTHORSHIP

FDL and JWS designed the study. JWS performed mathematical analysis. FDL performed the empirical data analysis. FDL and JWS wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY STATEMENT

All empirical data are available at https://github.com/fdelaend/data-analysis-data; all code used to perform the statistical analysis and Figs 1 and 4 are available at https://github.com/fdelaend/data-analysis. The programs to compute the model and make Figs 2 and 3 are available at https://github.com/juergspaak/EF-at-invariant-richness.

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