

Research

Do correlated responses to multiple environmental changes exacerbate or mitigate species loss?

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Biological communities face multiple global changes simultaneously, and predicting how they will respond remains a key challenge. Co-tolerance theory offers a framework for understanding how species-level responses to multiple stressors affect community properties. Co-tolerance theory predicts that positive correlations in species responses (i.e. species that are susceptible to one stressor are more likely to be highly susceptible to a second) lessen total species loss, essentially because species cannot be eliminated from a community twice. However, it is unclear whether several of the tenets of co-tolerance theory describe real-world communities, and what consequences result from such deviations. Here, we use an empirical dataset of bird community response to land-use change over a climate gradient to examine co-tolerance theory's tenet that environmental changes only harm species (not benefit them). We show that this tenet is not met, and then use simulations to examine how predictions of total species richness and community intactness vary when multiple environmental changes both harm and benefit particular species in the community. Finally, we conduct a sensitivity analysis, examining how the average species response to environmental change, as well as the variance among species, can further alter predictions. Overall, we find that predictions of co-tolerance theory can break down when communities contain species that benefit from some environmental changes. As a result, the presence of multiple environmental changes can either compound or mitigate species loss when species' responses are positively correlated, preventing a one-size-fits-all statement regarding the effects of correlated responses. This finding highlights the need to carefully consider the underlying mechanisms of community change when making policy assessments regarding the consequences of correlations of species responses to environmental impacts.

Keywords: global change, species loss, community

Introduction

A battery of rapid environmental changes is confronting biodiversity worldwide. These changes, including habitat conversion, climate change, environmental toxification, and hunting pressure from humans, are restructuring ecosystems and eliciting profound

biodiversity declines (Pereira et al. 2012, Dirzo et al. 2014, Newbold et al. 2015). Yet because species' responses to environmental changes are heterogeneous, community-level shifts are highly variable and difficult to predict (Supp and Ernest 2014). This complexity is further enhanced because communities rarely face one stressor at a time (Cote et al. 2016). Ascertaining how multiple environmental impacts interact remains a significant challenge (Mantyka-pringle et al. 2012, Cote et al. 2016). One path towards prediction necessitates first recognizing that species' responses to multiple environmental changes are often non-independent. Both positively correlated responses – where the same species are sensitive to multiple stressors – and negatively correlated responses – where species that are sensitive to one environmental changes are more tolerant, or even benefit from, another – have been reported in nature (Darling et al. 2013, McClanahan et al. 2014, Frishkoff et al. 2016). Co-tolerance theory provides a framework for explaining how positive and negative correlations in species responses may affect communities (Vinebrooke et al. 2004). Briefly, the framework posits that negatively correlated responses exacerbate local biodiversity loss because more species are affected when different species are sensitive to different stressors. With positive correlations, adding a second stressor affects the same species and fewer total species are expected to be lost locally. Yet the underpinnings of these expectations are primarily based on verbal arguments, and their generality has generally not been quantitatively explored (but see Brown et al. 2013).

Further developing co-tolerance theory requires examining several tenets about species and community-level responses to environmental change. First, what features of the community should be measured? Prior theory has largely focused on assessing how multiple stressors affect the total number of species in a community. Similarly, empirical studies have looked at how stressors affect functional groups within communities (Graham et al. 2011, Darling et al. 2013). However, community shifts can be measured in myriad ways that reflect alternative values or goals (Karp et al. 2015). For example, ecologists and conservationists may focus on either the richness, evenness, or composition of a local community (α -diversity) or the turnover between communities (β -diversity). Sometimes only pre-existing members of the community are deemed of ecological interest, and colonizing species discounted, because 'natural' compositional intactness is valued (Newbold et al. 2016).

Second, the nature of the environmental change must be considered. Classic co-tolerance theory holds that species responses are qualitative in nature – for a given amount of stress they either persist or go extinct. As such, stressors can only harm species (Vinebrooke et al. 2004), and when multiple stressors coincide, harm to individual species will plateau (at absence) and aggregate harm can only be compounded. Thus, colonization of new species from a regional species pool is not possible, because no species that is absent from the original local community can benefit from environmental change. We refer to this scenario as 'co-tolerance' throughout.

Overexploitation through hunting or fishing may in some cases represent a pure stressor since no species are directly benefitted (though indirect benefit is possible through competitive release; Dirzo et al. 2007).

Yet many environmental changes do not necessarily constitute 'stressors' in the standard sense of the word. Because species responses to environmental changes are often heterogeneous, some species actually benefit from environmental change (McKinney and Lockwood 1999, Warren et al. 2001, Supp and Ernest 2014, Frishkoff et al. 2015). As such, a strict 'co-tolerance' framework, in which species can only be harmed or remain unaffected, is likely not always the most appropriate means of understanding biodiversity change over time. Expanding our view of stressors by considering a diversity of responses to environmental change, while improving our analytical toolset to track how individual species responses build into community-level responses offers a promising path forward (Thompson et al. 2018).

A broader 'correlated response' framework allows for shifts in the environment that could simultaneously harm and benefit species. In a correlated response framework, environmental changes are allowed to act additively, each either increasing, or decreasing a species' total abundance at a site. There is thus the potential for compensatory responses – a species might be harmed by one environmental shift but benefited by another such that the net result is neutral (Fig. 1). Therefore, in a 'correlated response' model, a site's diversity will result from the net outcome of extinction and colonization from the regional species pool. Land-use change may often fall in this category when strong natural habitat affiliates are replaced by other species (Mendenhall et al. 2012, Morante-Filho et al. 2015, Frishkoff et al. 2016).

Under the co-tolerance framework, multiple stressors lead to minimum species loss if species' responses are positively correlated. This is because species that are locally extirpated by one stressor cannot be extirpated a second time in the presence of another stressor (Thompson et al. 2018). In contrast, a correlated response framework, could lead to the opposite outcome. Negative correlations might buffer individual species because the harm that they receive from the first environmental change may be offset by the benefit that they reap from the other. In contrast, if species responses are positively correlated, then species may only cross extirpation thresholds when exposed to multiple stressors (Fig. 1).

Here, we evaluate the role of correlations in species responses (or tolerances) on overall community diversity after two environmental changes by simulating communities under various assumptions regarding how species respond to the environment. To do so, we explore how correlated responses affect two types of α -diversity: total species richness and the proportion of the original community that persists through environmental changes. Total species richness comprises the entire community (minus extinctions and plus colonizations), whereas a focus on the 'original' species discounts colonizations (perhaps because colonizing species are considered 'weedy' or otherwise undesirable). To ground our

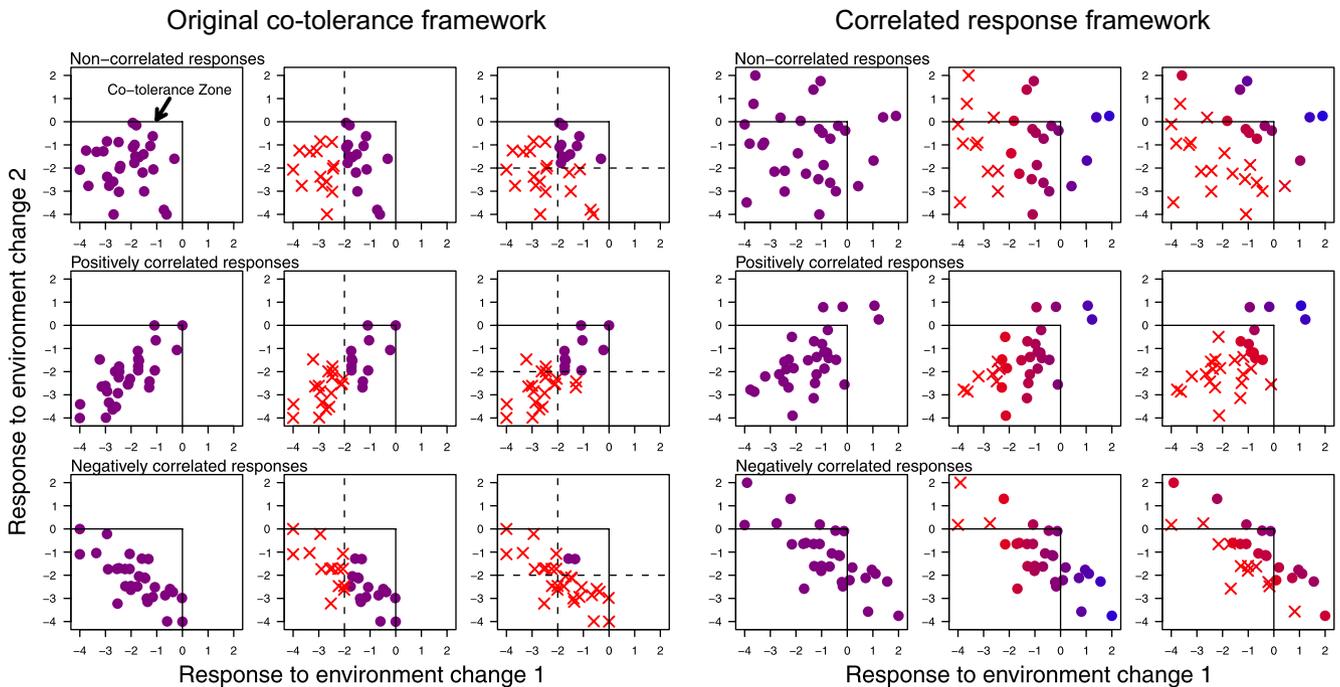


Figure 1. Species extirpation in a community under two hypothetical environmental changes, subject to either the original co-tolerance framework (Vinebrooke et al. 2004) or the correlated response framework described in this study. Under the original co-tolerance framework, species (points) always respond negatively to environmental changes (i.e. abundance responses are all < 0 , indicated by solid line ‘co-tolerance zone’). As a result a fraction of species is eliminated from the community under each change (extirpations indicated by red X) if they are not sufficiently tolerant (threshold indicated by dashed lines). The fraction of the community that survives is maximized when responses/tolerances to the two changes are positively correlated. Under a correlated response framework, species are allowed to change in abundance as a result of changing environments, with some species increasing (i.e. responses > 0) and others decreasing (i.e. responses < 0) in abundance. In the right hand panels, change in abundance is indicated by point color (blue: increasing abundance, red: decreasing abundance). For illustration, extirpation (red X) is assumed to occur when a species loses 90% of its population. Because species may suffer from the first environmental change, but benefit from the second, demographic rescue is possible – indicated by red X’s in second column transitioning to points in right most column. As a result, the fraction of the community surviving may be greatest under negative correlations of responses (in contrast to the original co-tolerance framework). Left, middle, and right panels in both frameworks represent (1) no environmental change, (2) only environmental change 1 occurring, and (3) both environmental changes 1 and 2 occurring.

analyses, we use a dataset of bird abundances across land-use (representing habitat conversion) and precipitation gradients (representing potential climate change) in Costa Rica. We first analyze the data to estimate the species response distributions – the means, variances and correlation describing how the meta-community as a whole shifts in response to land-use and climate change. We then examine whether the observed degree of correlation between responses to land use and climate exacerbates or mitigates species loss compared to a scenario in which responses to each environmental gradient are independent from one another. Finally, we explore how these patterns shift under a correlated response versus a co-tolerance model, and with contrasting magnitudes and variabilities in species’ responses to environmental change.

Methods

Overall approach

We used a simulation-based approach to vary 1) the degree to which environmental changes cause species loss (i.e. the

mean response), 2) the variation in species response to environmental changes, and 3) the degree of correlation between responses. To ground simulations, we used parameters values obtained from an empirical dataset of bird censuses along independent land-use and climate gradients in northwest Costa Rica, collected from June–August 2016. These data derive from a network of 20 forest-adjointing farms (Fig. 2, Supplementary material Appendix 1 Fig. A1), and include agriculture representative of the region: pastures ($n=12$), rice/melon crop rotations ($n=6$), sugarcane ($n=1$), and Taiwan grass (a forage crop, $n=1$). Point counts were conducted across 120 locations (6 per farm), with equal numbers in forested and deforested habitats along a precipitation gradient (1500 mm to 3000 mm total annual precipitation). Point count locations were separated by an average of 39 km, with sites in the same farm separated by an average of 580 m.

Sites were visited 1 or 3 times to maximize number of farms visited, while allowing estimation of detection probability, such that the true number of individuals of each species could be inferred from the data. Specifically, expert ornithologist (J. Zook) conducted all 20 min, 50 m radius

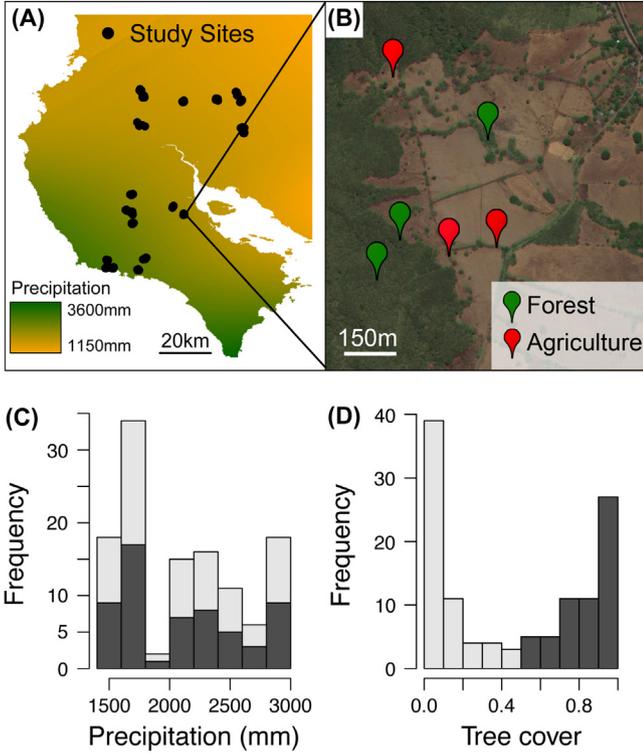


Figure 2. Map of study locations where bird communities were surveyed. (A) Study landscapes were arrayed across a regional precipitation gradient in northwestern Costa Rica. (B) An example landscape depicting how individual point count locations were distributed to vary the amount of local and landscape level forest cover. Histograms depict the distribution of sites along the precipitation gradient (C) and the local forest cover gradient (D) with sites within forest colored dark grey, and sites within agriculture colored white. Figure modified from Karp et al. (2018).

fixed distance point counts, recording all birds seen or heard throughout the survey period. Fly over birds were excluded.

Using hand classified aerial photographs, forest cover was quantified as the proportional area within 10 m buffers extending from 50 m to 1.5 km of each point count location. Mean total annual precipitation was modeled from nearby weather station data (Karp et al. 2018). The proportion of forest cover within each buffer distance, and precipitation, were centered and scaled by their standard deviation (e.g. subtracting the mean and dividing by the standard deviation) prior to analysis.

In the following sections, we discuss the model and resulting simulations in terms of ‘climate drying’ and ‘forest loss’ to connect them to the empirical dataset. While recent trends in Costa Rica have led to reforestation (Calvo-Alvarado et al. 2009), deforestation and habitat conversion to agriculture remain major threats to tropical biodiversity (Hansen et al. 2013). Regional precipitation regimes are expected to vary widely across the Neotropics, but northwest Costa Rica is expected to experience more

severe and frequent droughts in the future (Rauscher et al. 2008).

Estimating correlated responses from empirical data

We used a binomial mixture model to estimate species abundance responses to land-use and climate gradients while accounting for variation in detection (Royle and Dorazio 2008, Kéry and Schaub 2011). A full description of the modeling framework is contained in Karp et al. (2018). Briefly, for each species, the observed number of individuals at each site was modeled as a function of the unobserved true number of individuals, and the detection probability (P) of the i th species at the j th site during the k th visit. Detection was a function of a series of fixed-effect terms (α) including: the land-use type of the site (LU), the time of day ($time$), the presence of disruptive noise ($noise$), the number of humans in the vicinity of the site (ppl), the wind speed ($wind$), as well as species-specific random date effects (θ), and random intercept terms (δ) for species to account for other sources of variation. Specifically:

$$\text{logit}(P_{i,j,k}) = \alpha_0 \text{LU}_{[j]} + \alpha_1 \times time_{j,k} + \alpha_2 \times noise_{j,k} + \alpha_3 \times ppl_{j,k} + \alpha_4 \times wind_{j,k} + \theta_1 \times date_{j,k} + \delta_0 + \delta_1 \delta_{i,j,k}$$

The true number of individuals was assumed to come from a Poisson distribution, based on the expected number of individuals (Λ) of the i th species at the j th site, which was modeled according to:

$$\text{log}(\Lambda_{i,j}) = \beta_0 + \beta_1 \times deforest_j + \beta_2 \times dryness_j + \gamma_0 \delta_{i,j} + \gamma_1 \delta_{i,farm[j]}$$

Above $deforest$ is the (centered and scaled) amount of non-forest cover within 50 m of the point count, and $dryness$ (centered and scaled) is the negative mean annual precipitation of the site (so that positive values are more dry, and negative are more wet). We express variables as the inverse of forest cover and precipitation so that parameter estimates are directly interpretable as species response to anticipated future environmental changes – with positive values indicating population increases, and negative values indicating population declines. We additionally evaluated choice of spatial scale to confirm that 50 m was the correct spatial scale to gauge bird response to forest clearing (Supplementary material Appendix 1 Fig. A2). All α terms are simple fixed effects, while γ and δ terms were random intercepts (variance estimated from data around a mean of 0) designed to incorporate additional variation for each species, site, or replicate that could not be explained by other fixed and random effects. Parameters in the β and θ families were estimated for each species, with species terms drawn from a normal distribution of mean (μ) and variance (σ^2) estimated from the data.

β_0 was assumed to be independent of other terms, but β_1 and β_2 were not. Because we were interested in the degree

of correlation in responses to climate and land-use change, we allowed the degree of correlation in these terms to be estimated from the data. Specifically:

$$\begin{bmatrix} \beta_{1_i} \\ \beta_{2_i} \end{bmatrix} \sim \text{Norm} \left(\begin{bmatrix} \mu_{\beta_1} \\ \mu_{\beta_2} \end{bmatrix}, \begin{bmatrix} \sigma_{\beta_1}^2 & \rho\sigma_{\beta_1}\sigma_{\beta_2} \\ \rho\sigma_{\beta_1}\sigma_{\beta_2} & \sigma_{\beta_2}^2 \end{bmatrix} \right)$$

Where ρ represents the degree of correlation between a species land-use and precipitation responses, and μ and σ terms are the means and standard deviations estimated from the data.

Models were fit using MCMC, in the program JAGS, using vague priors throughout. Specifically, we used 4 chains, with 50 000 iterations per chain, a burn-in of 20 000 iterations, and a thin rate of 120, in order to generate a total of 1000 posterior samples. We checked for convergence by verifying that the Gelman–Rubin statistic was below 1.1 and by visually inspecting trace plots. We evaluated model adequacy using posterior predictive checks, which indicated reasonable model fit (Bayesian p-value=0.75; Supplementary material Appendix 1).

Testing correlated responses versus co-tolerance models

To understand whether our empirical data best fit a correlated response model (in which some species benefited from environmental change, even if many species were harmed), or a co-tolerance model (in which species can only be harmed), we examined the total posterior density of species responses that fell within parameter space governed by the co-tolerance model. Specifically, a co-tolerance model postulates that species respond negatively to both changes (i.e. all β_{1_i} and $\beta_{2_i} < 0$). We treat the proportion of the posterior distribution that falls outside of this zone as an indication of the relative performance of a more general correlated response model versus the more constrained co-tolerance model.

Assessing the importance of correlations in responses

To assess how correlation in responses to environmental changes affects community-level properties, we used key model parameters to simulate alternative scenarios. Specifically, we calculated the expected number of individuals at a site prior to environmental changes using the model formula excluding the random intercept components (since these relate to random, and therefore unpredictable site-specific properties).

$$\Lambda_i = \exp(\beta_{0_i} + \beta_{1_i} \times \text{deforest} + \beta_{2_i} \times \text{dryness})$$

A species was considered present if $\Lambda_i \geq 1$, and absent otherwise. This simulation was carried out under two states: 1) a ‘forest’ in a ‘wet’ region (deforest = -0.5, dryness = -0.5 with centered and scaled space), being converted to 2) a deforested area in a dry region (deforest = 0.5, dryness = 0.5). We focus on these conditions because co-tolerance theory is concerned with potential synergies arising from multiple environmental

changes occurring in tandem. We therefore do not explicitly analyze the two intermediate states (i.e. a deforested area in a wet climate and a forest in a dry climate).

To test the effect of correlated responses in the community-level diversity of the empirical data set, we simulated β_{0_i} , β_{1_i} and β_{2_i} 10 000 times, each time drawing them from distributions characterized by their corresponding mean (μ) and variance (σ^2) estimated from the data, but altering values of ρ (from -1, to 1, in increments of 0.1) to test the influence of the degree of correlation in responses. To test the effects of correlations more generally, we also systematically varied μ_{β_1} and μ_{β_2} , and/or $\sigma_{\beta_1}^2$ and $\sigma_{\beta_2}^2$.

Aspects of community change

We tracked two dimensions of community change. First, we quantified the total number of species present in each community (i.e. species richness; colonizations – extinctions). Second, we calculated the total number of species present in the community that persisted after environmental change (i.e. discounting colonizations).

We also examined the consequences of a co-tolerance version of our simulations. To do so, we simulated parameters as above, but truncated β_{1_i} and β_{2_i} so that they were forced to be less than or equal to 0. In this scenario, species could only maintain their prior abundances or decline in response to environmental change, such that the changes constituted ‘true stressors.’ Species could not benefit from ‘forest loss’ or ‘climate drying’ and colonization of previously absent species was therefore impossible. Consequently, each site’s species richness and the total number of species originally present in the community were necessarily equivalent in the co-tolerance framework.

Data deposition

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.7c652r8>>. (Frishkoff et al. 2018).

Results

Do the data better support a co-tolerance or correlated response model?

We found strong evidence that a correlated response model better explains patterns in Costa Rican bird diversity than a co-tolerance model (64% of posterior density of responses was in a region of parameter space excluded by the co-tolerance model; Fig. 3, Supplementary material Appendix 1 Fig. A3). Further, many individual species respond positively to land-use change: the posterior mean estimated response to land-use change of 48% of species was positive, with 20% clearly reaching maximum abundance in deforested habitats (95% Bayesian credible interval of species’ estimate excluded 0). Similarly, 39% responded positively

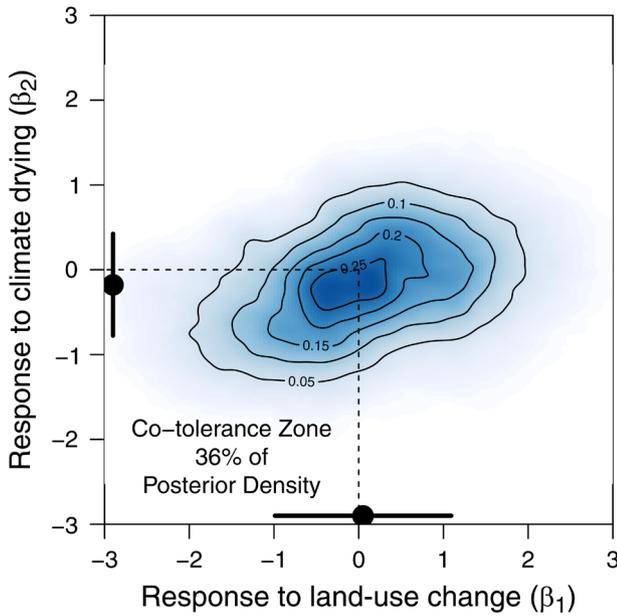


Figure 3. Bird species responses to land-use and precipitation in Costa Rica. Colors and contours indicate posterior density of community-wide response to environmental changes. Black points along axes depict model-estimated mean responses across species, and bars indicate the standard deviation across all species. Parameter values (e.g. β_1) are interpreted as the expected log-scale abundance response resulting from one SD of altered environmental conditions (loss of ~40% forest cover, or loss of 464 mm of rainfall). The figure demonstrates that a correlated response model better describes the relationship between land-use change and climate drying in Costa Rican birds. Fully 64% of the posterior density of species response lies outside of parameter space permitted by a co-tolerance model. Responses to environmental changes are positively correlated in this dataset, with species likely to decrease in abundance in response to climate drying also more likely decrease in response to land-use change.

to climate drying, though only 3% could be classified as dry climate affiliates with certainty (95% BCI excludes 0). The mean response of species (in units of log response) was 0.05 [95% BCI: -0.17, 0.26] for deforestation (average of distribution responds negatively to forest cover, though non-significantly), and -0.18 [95% BCI: -0.32, 0.03] for drying (average of distribution responds positively to wetter climates). Finally, species responses to climate drying and land-use conversion were positively correlated ($\rho = 0.35$ [95% BCI: 0.08, 0.57]).

Correlation in responses and community change

Do positively correlated responses to land use and drying exacerbate or mitigate species loss? Using parameter estimates from the data, we simulated communities before and after habitat conversion and climate drying, varying only the degree to which responses were correlated. In this model, the degree to which species exhibit correlated responses did not

notably affect the total number of species present because colonization by dry and agriculture-affiliated species balanced extinction of wet climate and forest species (Fig. 4). However, the proportion of species in the original community that persisted after environmental change was influenced by the strength of correlation. The degree of correlated responses observed in the bird dataset was responsible for 6% more species being lost than would be lost if species did not exhibit correlated responses, and >25% more species loss than if responses were perfectly negatively correlated (Fig. 4).

But would these patterns persist if species behaved according to a co-tolerance model? In the co-tolerance scenario, the response parameters of species that were predicted to benefit from climate drying or forest loss were set to 0 such that they functionally did not respond to either stressor. In this scenario, the effect of positively correlated responses flipped – fewer species were lost when land use and climate drying negatively affected the same species than when land use and climate drying affected different species.

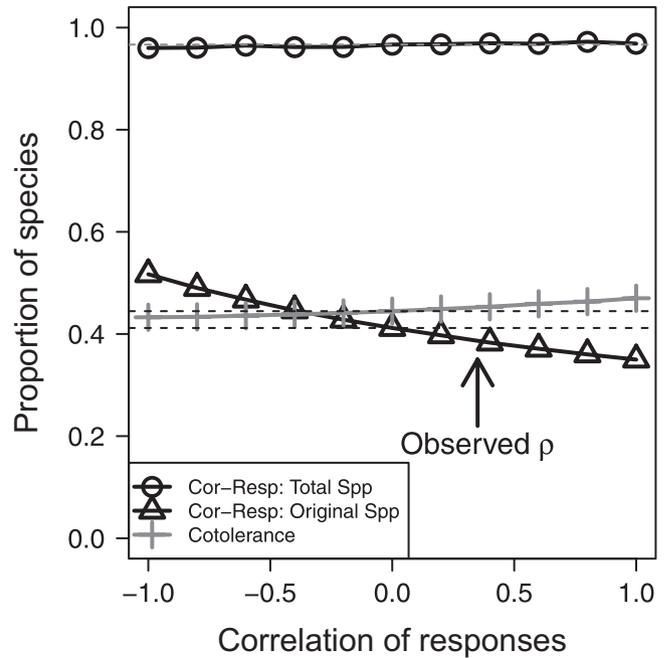


Figure 4. Model simulations of the effect of the degree of correlated responses on species loss under tree cover loss and climate drying. Each point represents the mean proportion of the post-impacted community compared to the pre-impacted community across 10 000 simulations. ‘Cor-resp’ applies to a model in which species can both increase or decrease in response to environmental changes (the model that is best supported by the data), whereas ‘Co-tolerance’ applies to a situation in which species can only be harmed by environmental change. ‘Observed ρ ’ depicts the degree of correlation in responses actually detected in the bird dataset. Among Costa Rican birds, greater species loss occurs from the original community when responses to environmental changes are positively correlated. Horizontal dashed lines indicate the proportion of species maintained when there is no correlation between responses to the two environmental changes (i.e. $\rho = 0$).

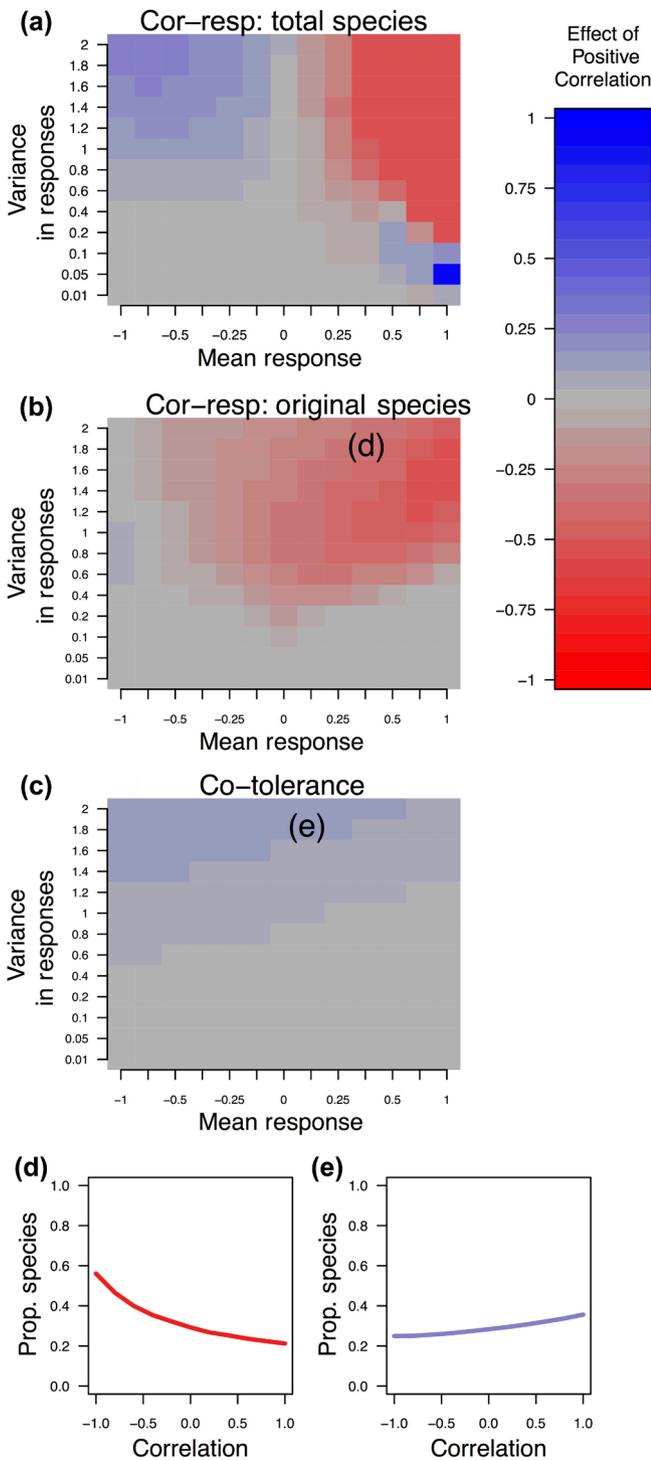


Figure 5. Heatmaps depicting how correlation between responses to environmental changes lead to heightened or diminished species loss in communities depending on both the average species response, and the variation in species responses. (a) Positive correlations in species' responses can lead to either greater, or fewer total species in communities, largely dependent on the mean meta-community response to the environmental change. (b) Under the correlated response model, the proportion of species from the original community tends to decline when responses are correlated across most

Sensitivity to mean responses and variation among species responses

We conducted a sensitivity analysis to determine whether positive correlations in responses always lead to more species loss, and positive correlations in tolerance always lead to less species loss. We did so by systematically varying the other principal parameter groups in the model – the mean response across species to each of the environmental changes (μ_{β_1} and μ_{β_2}), and the variation among species around this mean response (σ_{β_1} and σ_{β_2}).

We found that the effect of correlation of responses depended both on the overall model of community loss (i.e. correlated response versus co-tolerance) as well as other parameter values (Fig. 5). We first focused on total species richness under the correlated response model. Here, the effect of correlation hinged on the mean response across the metacommunity (Fig. 5a). When the mean response resulted in the average species increasing in abundance after drying or forest loss (i.e. μ_{β_1} and $\mu_{\beta_2} > 0$), positively correlated responses resulted in lower species richness (i.e. even though species richness tends to increase after environmental change, this increase is least when responses are positively correlated). However, when the average species in the metacommunity responded negatively to drying and forest loss, the effect flipped, and negative correlations in species responses resulted in the lowest species richness (i.e. positively correlated responses mitigate species loss). Patterns differed if only species from the original community were considered. In this case, positive correlation of responses almost always led to excessive extinction up until the point of very extreme species loss (Fig. 5b). Finally, under the co-tolerance model, most parameter values caused positive co-tolerances to result in less severe species losses (Fig. 5c). In nearly all cases, increasing variation between species in their responses (σ_{β_1} and σ_{β_2}) led to more extreme effects of correlated responses and species loss.

Discussion

Effects of correlations of responses

We found that positive correlations in species responses to multiple environmental changes do not always reduce

Figure 5. (Continued)

parameter combinations. (c) In contrast if responses are correlated under the co-tolerance model then fewer species are lost. In (a–c) colors correspond to the expected increase (red) or decrease (blue) of species lost by increasing the correlation coefficient by from completely negatively correlated ($\rho = -1$) to completely positively correlated ($\rho = 1$) in units of proportions of the original community. For example, a red cell with a value of -0.3 means that a flip from negative correlated responses to positive correlations will result in 30% more species being lost. (d) and (e) illustrate how the proportion of species that survive after environmental change varies depending on the correlation of response, for specific parameter combinations from (b) and (c).

species loss, as predicted in classic ‘co-tolerance’ theory (Vinebrooke et al. 2004). Both the underlying model of species response (i.e. ‘co-tolerance’ versus ‘correlated response’) and the metric of species loss (total richness versus community intactness) greatly influenced the consequences of correlations. This variation occurred even in our comparatively simple model, where impacts of environmental changes on species abundances could only be additive (and not interactive). Indeed, even within a single model, other characteristics of species’ responses (i.e. the mean and variance of response distribution across the species pool) governed the magnitude and direction of the effect. As a result, no single statement regarding the consequences of correlated responses on community resilience during environmental change can be made. Instead, a more nuanced approach is needed, in which each of the core assumptions that generate community impacts are considered in turn.

The first issue is whether a ‘correlated response’ or strict ‘co-tolerance’ model best describes responses to environmental change. Under a co-tolerance model, where environmental changes never benefit species and effects of multiple changes are additive, positive co-tolerance almost invariably leads to a reduction in species loss (as predicted in co-tolerance theory). However, under a correlated response model, where species can suffer from one environmental change but benefit from another, the effect of correlations can either mitigate or exacerbate species loss.

Some environmental changes may represent true stressors and better fit a co-tolerance model. True stressors are especially likely to occur when environmental changes are quantitatively extreme, or qualitatively different from conditions that species evolved under, such that no species are likely to benefit. In some areas, climate change could represent a true stressor: for example, when warming occurs in an already warm region that cannot draw upon a species pool of even warmer adapted species for colonization. However, even if the environmental changes themselves represent stressors for all species, tolerant species may indirectly benefit as a result of competitive or predator release. In this scenario a ‘correlated response’ framework would better describe the system than the original co-tolerance response.

Many studies of communities exposed to climate change, land-use change, or other human impacts are increasingly reporting only modest species richness losses, or none at all, even as species composition changes radically (McGill et al. 2014, Supp and Ernest 2014, Dornelas et al. 2014, Magurran et al. 2015, Morante-Filho et al. 2015). These findings highlight that, for many environmental changes, some species will benefit and others will decline, placing such communities firmly in ‘correlated response’ parameter space. An implicit adoption of a strict ‘co-tolerance’ model is thus problematic, as it may lead to the false generalization that positively correlated responses to multiple environmental changes always benefit communities. Making this incorrect assumption could lead practitioners to forego interventions designed to mitigate one of many stressors that threaten

positively-correlating communities, when it is precisely these communities that would benefit most from targeted actions (Brown et al. 2013).

Our results also demonstrated that the impact of correlated responses hinges on the metric of biodiversity loss examined, e.g. total species richness versus the proportion of species from the original community that persists. Ultimately, positive correlations increase community turnover rates, causing more species from the original community to be locally extirpated but also increasing colonization from the regional species pool. Whether community response is more appropriately measured as total, versus original species richness, will vary according to overarching conservation goals (Karp et al. 2015). Globally, however, community composition is increasingly considered a more appropriate focus of conservation than species richness, in part because species that benefit from environmental change will likely do so similarly across the globe, depressing β -diversity and contributing to large-scale biotic homogenization (degrading γ -diversity), even if α -diversity remains constant (McKinney and Lockwood 1999, McGill et al. 2014, Dornelas et al. 2014, Socolar et al. 2015).

Beyond the aspect of biodiversity considered, our results demonstrated that the form of species response distributions may also determine the consequences of correlated responses (particularly for total species richness). For example, we found that when the average species’ abundance increases in response to an environmental change (mean response > 0), positively correlated responses lead to relatively lower species richness. However, when species decrease on average (mean response < 0), positively correlated responses can lead to greater species richness than when responses are uncorrelated. However, there are combinations of means and variances of species response distributions for which correlations yield no appreciable effect on species loss (Fig. 5), even though the absolute number of species lost can be quite large (as in Fig. 4). Unlike choosing a conservation priority, or guessing as to whether a ‘correlated response’ or ‘co-tolerance’ framework applies to the environmental changes at hand, these aspects of the species response distribution (along with the empirical degree of correlation) must be measured in the field, based on how actual species respond.

Limitations and future directions

By using bird censuses to quantify the response distribution (means, variances and correlation) of the regional species pool, we were able to simulate data at individual sites, while varying each characteristic of the response distribution independently. This approach is highly generalizable, but suffers from a few key limitations. First, field data are needed to robustly characterize species response distributions, prohibiting the applicability of our approach to poorly-studied regions. This will become less of a hindrance as more high-quality datasets are made available (Hudson et al. 2016), or as trait-based or phylogenetic methods allow accurate inferences regarding how data deficient species respond to changes

like habitat conversion (Frank et al. 2017, Nowakowski et al. 2018). Second, not all environmental changes can be measured directly. Here, inferring combined effects of land-use and climate change required assuming the appropriateness of a space-for-time substitution. Specifically, we assumed that dispersal limitation did not limit colonization ability, such that any species could colonize a site from the regional species pool if and when environmental change made the site more suitable. The small spatial extent of our precipitation gradient (all sites within 79 km of one another) and the absence of mountain ranges or other major geographic barriers makes this a reasonable assumption. Another major assumption of the space-for-time approach is that future climate change will occur in a manner similar to the existing environmental gradients. Namely, variation in total annual rainfall will be the primary force structuring future communities. While a decrease in rainfall is likely (Rauscher et al. 2008), there is a large degree of uncertainty regarding spatial rainfall patterns across climate models (Magrin et al. 2014). As such, it is also possible that regional rainfall may increase, which in turn will mean that species' responses to land-use and climate change will be negatively, not positively, correlated. This uncertainty makes predictions related to climate change particularly challenging. Finally, the space-for-time substitution focuses on long-term community composition, after colonization and extirpation have worked themselves out. Over shorter time scales, before increased fecundity or immigration can bolster populations of 'winners' under rapid environmental change, a co-tolerance framework may better describe community dynamics.

However, perhaps the largest limitation is underlying uncertainty about the true model of environmental change. Beyond 'co-tolerance' versus 'correlated response', subtler model assumptions may also matter. For example, our model assumes that species responses to both environmental gradients are linear, and that variation between species can be approximated as a multivariate normal distribution. In nature, however, species responses to local land-use, climate, and other environmental gradients may be non-linear, such that they display thresholds, or possess defined optima (Tingley and Beissinger 2013, Frishkoff et al. 2015). Moreover, while in our case we assumed additivity of species responses between land-use and climate change, populations and communities often have non-additive (synergistic or antagonistic) responses to multiple environmental changes (Crain et al. 2008, Darling and Côté 2008, Jackson et al. 2016), reducing the appropriateness of the simplest conceptual models. Future work would profitably focus on addressing and relaxing these assumptions by incorporating non-linear effects, and interactions between environmental changes at the species level. This task will be facilitated by advances in statistical community modeling that have granted researchers the ability to robustly characterize species response distributions in communities (Ovaskainen and Soininen 2011, Iknayan et al. 2013, Hooten and Hobbs 2015, Warton et al. 2015, Ovaskainen et al. 2017), but must also be met with theoretical advancements that guide our expectations on the

functional forms of nonlinearities, and the degree to which interaction effects correlate with the additive components of response to environmental change.

Finally, future work dedicated to understanding the effects of correlated responses must expand beyond considering simple metrics of taxonomic diversity. Other aspects of diversity often matter, such as functional or phylogenetic diversity, especially when maintenance of ecosystem function is a primary management or conservation goal (Cadotte et al. 2012, Mouillot et al. 2013, Thompson et al. 2015). If different functional groups, or alternative phylogenetic clades, respond deterministically to multiple environmental impacts, then the magnitude and direction of functional or phylogenetic diversity loss may deviate from that predicted by taxonomic loss (Purvis et al. 2000, Vinebrooke et al. 2004, Mouillot et al. 2013). Similarly, local environmental impacts may reverberate to landscape and regional scales in ways that are not predicted by local effects (McGill et al. 2014). Expanding consideration of how multiple environmental changes will affect β - and γ -diversity is needed to ascertain the full biological impact of correlated responses.

Conclusion

Environmental impacts rarely occur in isolation. Thus, understanding the effects of multiple simultaneous environmental changes on species and communities is necessary to predict and address ongoing threats to biodiversity. Unfortunately, our knowledge of the extent to which multiple impacts interact is still limited. Correlation in how species respond to environmental changes has long been recognized as important (Vinebrooke et al. 2004). Our work demonstrates that the effect of such correlations is not as straightforward as originally theorized, and that species loss is not always mitigated when responses are positively correlated. However, some predictability can be gained by defining the metric of conservation interest and by recognizing the types of environmental changes that species face. Greater understanding of ecological responses to environmental change will benefit from a quantitative understanding of how species responses are distributed in real-world communities, and whether particular changes represent universal stressors, or whether compensatory responses between changes result in winner-loser dynamics. Incremental improvements in the theory behind correlated responses and co-tolerance, coupled with ongoing empirical data collection, may yet result in truly generalizable patterns across taxa, regions, and environmental impacts.

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Supplementary material (available online as Appendix oik-05288 at <www.oikosjournal.org/appendix/oik-05288>). Appendix 1.