Predicting ecosystem vulnerability to biodiversity loss from community composition

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Abstract. Ecosystems vary widely in their responses to biodiversity change, with some losing function dramatically while others are highly resilient. However, generalizations about how species- and community-level properties determine these divergent ecosystem responses have been elusive because potential sources of variation (e.g., trophic structure, compensation, functional trait diversity) are rarely evaluated in conjunction. Ecosystem vulnerability, or the likely change in ecosystem function following biodiversity change, is influenced by two types of species traits: *response traits* that determine species' individual sensitivities to environmental change, and *effect traits* that determine a species' contribution to ecosystem function. Here we extend the response-effect trait framework to quantify ecosystem vulnerability and show how trophic structure, within-trait variance, and among-trait covariance affect ecosystem vulnerability by linking extinction order and functional compensation. Using in silico trait-based simulations we found that ecosystem vulnerability increased when response and effect traits positively covaried, but this increase was attenuated by decreasing trait variance. Contrary to expectations, in these communities, both functional diversity and trophic structure increased ecosystem vulnerability. In contrast, ecosystem functions were resilient when response and effect traits covaried negatively, and variance had a positive effect on resiliency. Our results suggest that although biodiversity loss is often associated with decreases in ecosystem functions, such effects are conditional on trophic structure, and the variation within and covariation among response and effect traits. Taken together, these three factors can predict when ecosystems are poised to lose or gain function with ongoing biodiversity change.

Key words: biodiversity loss; compensation; disassembly; ecosystem function and services; functional diversity; functional traits; resilience; resistance; vulnerability.

INTRODUCTION

Biodiversity change is a central feature of the Anthropocene and is compromising the magnitude and stability of many ecosystem functions, threatening both the systems themselves and the essential services they provide (Naeem et al. 2012). Species responses to external drivers (e.g., climate change, over-exploitation, habitat fragmentation) are mediated by specific traits such as body size, dispersal ability, and thermal tolerances, and thus, to a degree, are predictable (Payne et al. 2016). In contrast, ecosystem responses to biodiversity loss can vary widely, with some functions changing dramatically, while others remain unaffected or even increase (Bunker et al. 2005, Oliver et al. 2015). Potential sources of this variation include how individual species contribute to function, the identity of extinct species, community trophic structure, and how populations fluctuate with external drivers; however, these factors are rarely explored in traditional biodiversity-ecosystem function experiments. Despite the emerging scientific consensus on the mechanisms underpinning the impacts of biodiversity on ecosystem properties, linking species processes to the ecosystem scale to forecast how functions respond to altered biodiversity remains a challenge (Cardinale et al. 2012, Tilman et al. 2014).

Estimating the degree to which ecosystem function is likely to change due to biodiversity loss, an ecosystem property which we term *ecosystem vulnerability*, is critical for understanding why ecosystems vary in their response to ongoing environmental change. Ecosystem vulnerability depends on the order in which species are lost from a community (i.e., dissasembly; Ives and Cardinale 2004, Zavaleta et al. 2009), the functional contribution of individual species (Suding et al. 2008, Díaz et al. 2013), intraspecific variation, and how remaining species in a community may compensate for biodiversity change (Naeem 1998, Thomsen et al. 2017). The response-effect trait framework has been frequently used to link traits that increase an individual species' sensitivity to external drivers (response traits) to how they contribute to function (effect traits; Lavorel and Garnier 2002). While response traits can be used to predict the order of community disassembly, effect traits can be used to predict the change of function associated with species loss or gain (Lavorel and Garnier 2002, Suding et al. 2008, Díaz et al. 2013). As such, when response and effect traits covary positively, large decreases in ecosystem function can be expected with ongoing biodiversity loss. However, a central feature of multitrophic communities is their ability to compensate for changing composition, and extending trait-based frameworks to quantify ecosystem vulnerability also requires

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predicting how species functional contributions change in response to alterations in community composition (Connell and Ghedini 2015, Thomsen et al. 2017).

The ability of communities to functionally compensate in response to biodiversity change is associated with community level compensatory dynamics, which can cause aggregate community biomass or density to remain stable despite changes in community composition (Peres and Dolman 2000, Gonzalez and Loreau 2009). As a process, compensation is associated with a number of community properties, including how niche differences and competitive interactions are distributed across a community (Ives and Cardinale 2004). Trophic structure can thus determine biomass compensation by limiting competitive release associated with changing community composition to specific trophic levels (Gonzalez and Loreau 2009). Similarly, functional compensation might be restricted in multitrophic communities if response and effect traits are clustered based on trophic level. For example, high-level consumers can be characterized by shared response traits (e.g., large body size) that are correlated with shared effect traits (e.g., long distance seed dispersal; Peres et al. 2016). As a result, functions associated with specific trophic guilds might be irreplaceable by species in other trophic levels. In contrast, if trophic level is unrelated to how species contribute to function, trophic structure could have little impact on ecosystem vulnerability by not restricting functional compensation to specific guilds. While the effect of compensatory dynamics on community properties has received considerable attention (Gonzalez and Loreau 2009, Connell and Ghedini 2015, Thomsen et al. 2017), trait-based approaches rarely consider their role in maintaining ecosystem function with ongoing biodiversity change.

In addition to trophic structure, the community-level frequency distribution of species traits has received little attention although it could strongly affect functional compensation and by extension, ecosystem vulnerability. Changes in species composition can alter ecosystem function even if compensatory dynamics cause total biomass to remain stable, because of functional trait differences between species. When the contributions of species to ecosystem function are driven by dominance rather than because of their unique effect traits, biomass compensation should mitigate the impact of changing species composition on ecosystem function (Davies et al. 2011, Pan et al. 2016). However, biomass compensation will not ensure resilient ecosystem functions when effect traits between the extinct and extant species are different (i.e., trait redundancy; Naeem 1998, Oliver et al. 2015). While traits are often assumed to be normally or uniformly distributed within communities (Díaz et al. 2016), alternative distributions are also common (e.g., lognormal; Savage et al. 2007). Thus, a community's trait frequency distribution can have strong implications for functional compensation and consequently, ecosystem vulnerability.

Beyond linking a species' sensitivity to change to their contribution to function, the covariation between response and effect traits also links extinction order and compensation. In both plants and animals, trait tradeoffs are ubiquitous, with community-scale trait covariation affecting a number of community processes (e.g., assembly, succession; Winemiller et al. 2015, Díaz et al. 2016). However, how community-scale trait covariation affects the response of

function to biodiversity loss, by linking community processes (i.e., extinction and compensation) to ecosystem properties (i.e., ecosystem vulnerability), is underexplored. Empirical evidence suggests that traits that make a species more sensitive to external drivers (e.g., body size) often covary with traits that increase their contribution to function (e.g., pollination rates, nutrient excretion rates; Larsen et al. 2005, McIntyre et al. 2007), but this covariation can also be negative or non-existent, resulting in alternate relationships between species change and ecosystem responses, which are rarely considered in conjunction with compensation. Exploring the consequences of these different trait relationships in conjunction with the distribution of traits across multiple trophic levels is critical for gaining insight into why some ecosystem functions change so drastically with biodiversity loss, while others remain resilient, and may facilitate prediction of ecosystem responses to environmental change.

We develop a framework for estimating ecosystem vulnerability based on linking processes across species- (contribution to function and species vulnerabilities), community- (compensatory dynamics and disassembly) and ecosystem-scales (ecosystem vulnerability). Based on this framework, we evaluate the relationship between biodiversity and ecosystem vulnerability by developing an "ecosystem stress test," in silico trait-based simulations for evaluating the outcomes of different extinction scenarios on ecosystem function. Each scenario quantifies ecosystem vulnerability by identifying the number of species needed to maintain ecosystem function above a set threshold. We then test the framework through simulations that employ a range of common community-scale trait frequency distributions (normal, uniform, and lognormal) as well as different degrees of covariation between response and effect traits (positive, negative, and non-existent). Through these simulations, we bridge across species, community and ecosystem scales, linking common species-level metrics to ecosystem vulnerability, and begin to decipher the implications of changes in biodiversity for maintaining ecosystem function. Specifically, through our simulations we asked:

1) To what extent can compensation reduce ecosystem vulnerability?
2) How does trophic structure influence compensation outcomes, and consequently, ecosystem vulnerability?
3) What role does community-level covariance between response and effect traits play in influencing ecosystem vulnerability?
4) How does the distribution of trait values within a community affect ecosystem vulnerability?
5) How well do community-scale vulnerability properties (sensu Weeks et al. 2016) predict ecosystem vulnerability?

Biodiversity is often assumed to increase the resistance and resilience of ecosystem function to biodiversity loss (Oliver et al. 2015). However, increasing biodiversity can increase community vulnerability since more speciose communities are likely to include functionally distinct and sensitive species (Mouillot et al. 2013, Weeks et al. 2016). By examining how traits mediate the interaction between extinction order and functional compensation, our framework integrates the effect of resistance and resilience on ecosystem function in natural systems. Additionally, numerical models that input trait data

to predict ecosystem vulnerability are often difficult to apply across ecosystems. In contrast, we provide an unbiased method to predict the ability of ecosystems to provide services despite ongoing biodiversity loss, which can be achieved empirically by collecting relevant information on response and effect traits together with community trophic structure. Ultimately, scaling existing species-based approaches to the ecosystem level using the ecosystem stress test developed can enable rapid assessments of the impact of biodiversity change on the ability of ecosystems to maintain function and provide services that are central to human wellbeing.

METHODS

Contribution to function

We assume that species i contributes to a function a ($F_{a,i}$) via an effect trait ($E_{a,i}$) and the species' biomass in the system (m_i) (following Lavorel and Garnier 2002, Solan et al. 2004, Bunker et al. 2005), such that the total function, T_a, in a community with S species, is

$$T_a = \sum_i^S F_{a,i} \qquad (1)$$

where

$$F_{a,i} = m_i E_{a,i}. \qquad (2)$$

This approach assumes that for all species, $F_{a,i}$ is linearly related to m_i and $E_{a,i}$, and yields units related to the particular function (e.g., grams of carbon per unit mass). While this approach only considers mass ratio effects (sensu Grime 1998), and thus does not explicitly account for the impacts of species interactions on their contributions to function, it is flexible, with the potential to be expanded to include multiple functions.

Species-level vulnerability index

Individual species vulnerabilities were calculated as a function of each species' exposure to a threat, and the species-specific sensitivity:

$$V_{i,k} = \varepsilon_k R_{i,k} \qquad (3)$$

where $V_{i,k}$ is the vulnerability of species i to external driver k, ε_k is the exposure of species i to driver k, and $R_{i,k}$ is the response trait of species i associated with the driver k. Exposure varies across landscapes, and thus vulnerabilities are expected to vary across a species' range. This equation assumes that all species are spatially bound in one community, and thus all species face the same exposure to a threat. However, species differ in their sensitivities, and $V_{i,k}$ provides a relative extinction probability for all species within a community based on exposure and sensitivity. When evaluated at a community scale, these vulnerability indices provide a means for developing probabilistic scenarios of species loss from a community.

Ecosystem stress test

We simulated communities in which we varied the community scale trait frequency distributions together with the strength of covariation between response and effect traits. We assumed that there was only one stress and set the exposure at 1, such that all species experience the same level of the threat. These simplifying assumptions allowed us to specifically analyze the role of trophic structure, trait distribution and covariance on compensation outcomes, while holding all other factors constant. Thus, relating vulnerability and contribution to function relied on fitting the following relationship:

$$R_{i,k} = \alpha m_i E_{a,i} \qquad (4)$$

where α describes the correlation between $V_{i,k}$ and $F_{a,i}$, which in this case is directly determined by the covariation between response and effect traits ($R_{i,k}$ and $E_{a,i}$ respectively). We factorially manipulated trait distributions (uniform, normal, and lognormal) and covariation between traits (i.e., $\alpha = 1$, 0, -1) so that 500 simulated communities were created for each of the nine different trait scenarios. Subsequently, F_i and V_i were scaled so that all species had values between 0 and 1 by dividing every species by the maximum value in each community. Additionally, in each of the communities, all species were assigned as primary producer, herbivore or predator based on the ratio of 7:2:1. This ratio was chosen to maintain sufficient variability in trophic structure while approximating an ecosystem dominated by lower trophic levels. To explore how trophic structure influences compensation outcomes, we assigned trophic identity both randomly and such that it was positively related to V_i. The values used in all simulations are detailed in Table 1.

We applied an ecosystem stress test to each of the communities to determine the ecosystem's vulnerability, which was quantitatively evaluated as the number of species needed to maintain functioning above a defined threshold (Fig. 1). This trait-based simulation approach relies on modeling species extinction scenarios such that the probability of a species being lost from a community is directly proportional to

TABLE 1. Symbols and parameter values used in the simulation.

Symbol	Explanation	Value in the simulation
T_a	Total ecosystem function a	Specified by Eq. 1
$F_{a,i}$	Contribution to function a by species i	$F_{a,i} = m_i E_{i,a}$
S	Number of species	$S = 100$
m_i	Mass of species i	$m_i = F_{a,i}/E_{i,a}$
$E_{a,i}$	Effect trait linked to function a of species i	$E_{a,i} \sim$ rnorm[0,1], runif[0,1], rlnorm[0,1]
TG	Trophic guild	Allocated either randomly to all species in a community in the ratio of 7:2:1, or correlated with $V_{i,k}$
$V_{i,k}$	Vulnerability of species i to driver k	$V_{i,k} = \varepsilon_{i,k} R_{i,k}$
$\varepsilon_{i,k}$	Exposure of species i to driver k	$\varepsilon_{i,k} = 1$
$R_{i,k}$	Response trait of species i linked to driver k	$R_{i,k} = E_{i,k}, -E_{i,k}$, runif[0,1]

the vulnerability of that species ($V_{i,k}$; Eq. 3). At each time step, a species is first lost and the remaining total function (T_a; Eq. 1) is measured, without compensation. Subsequently, the remaining species compensate for the lost biomass associated with the extinct species based on two replacement scenarios: random replacement (i.e., all remaining species have same probability of replacing extinct species) and trophic guild replacement (i.e., only remaining species within the same trophic guild are able to replace extinct species). These replacement rules assume that the biomass of an extinct species is allocated to the compensating species, and in the scenario including trophic guild replacement rules, once the last member of a trophic guild is extinct, the biomass in the system is lost (Solan et al. 2004, Bunker et al. 2005, McIntyre et al. 2007). Finally, the number of species, as a proportion of the total initial species richness, needed to maintain function above a set threshold of initial function is evaluated. The choice of threshold can be manipulated, and this provides a comparable measurement of vulnerability between different communities such that the higher the number of species needed to maintain function above a threshold, the higher the ecosystem vulnerability. To analyze and compare ecosystem vulnerability across a range of communities (see below), we set the function threshold at 75%, 50% and 25% ($S_{T=75}$, $S_{T=50}$ and $S_{T=25}$ respectively).

Analysis of relationship between community level properties and ecosystem vulnerability

We calculated the total community vulnerability (V_{TOT}) by summing the vulnerabilities of all species within each of the initial simulated communities (Weeks et al. 2016). Given that these community vulnerabilities are not independent from functional diversity, to characterize the variation in community vulnerability of the simulated communities, we used the standard deviation of the whole community vulnerability (V_{SD}) as well as the mean vulnerability in the community (V_{Mean}). We fit linear models with the different thresholds (e.g., $S_{T=50}$) as the response variable and either V_{TOT}, V_{SD} or V_{Mean} as the predictor variable for each replacement scenario. These relationships were analyzed for communities with positive trait covariation (i.e., α = 1) to explore the relationships between vulnerability and function in communities that always lost function with decreasing biodiversity. All analyses and simulations were conducted in R (R Core Team 2016; see Data S1 for simluation code).

RESULTS

Across all simulated communities, compensation reduced ecosystem vulnerability by decreasing the proportion of
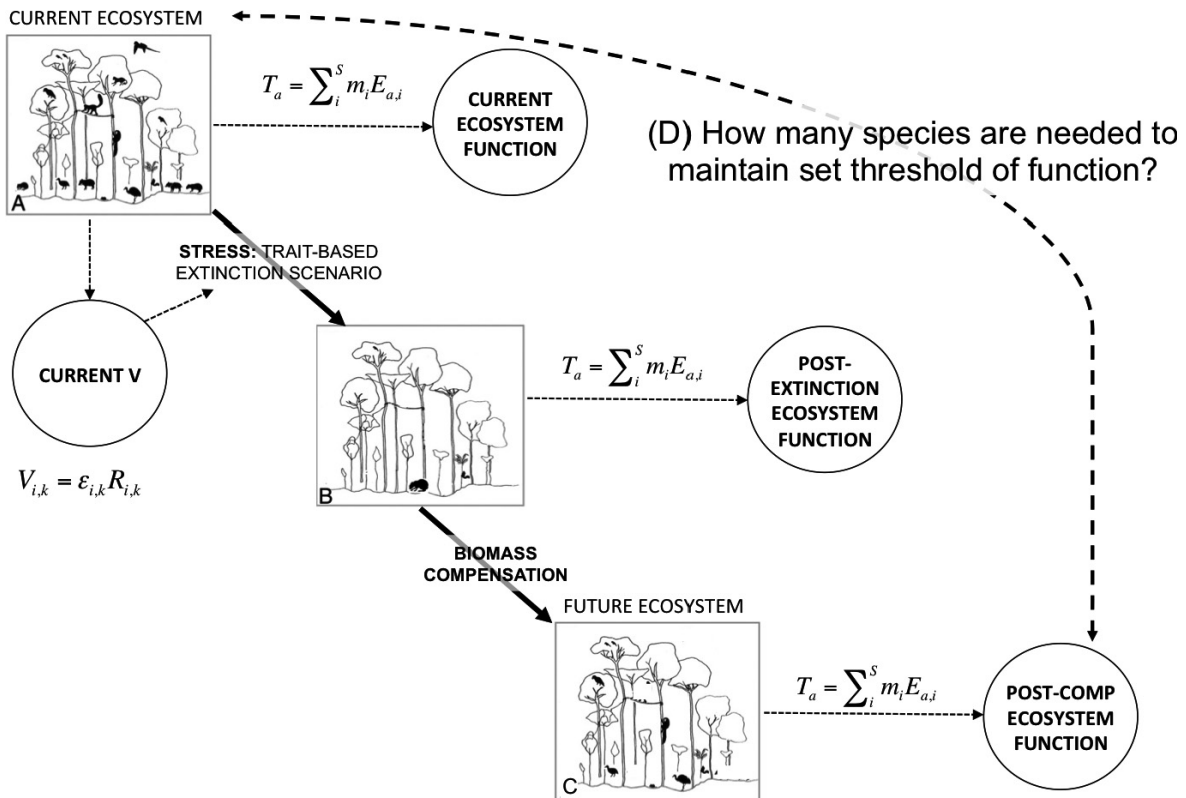

FIG. 1. The ecosystem stress test to quantify ecosystem vulnerability. In the first step (A), we obtain the total current ecosystem function, and use the species vulnerabilities to seed the probabilistic trait-based extinction scenarios. In the second step (B), a stress is applied whereby a species is lost and the post-extinction ecosystem function is measured without compensation. In the third step (C), biomass compensation is modeled by allocating the lost biomass associated with the extinct species to a remaining species based on replacement scenarios (see *Methods*). Finally, after all species are extinct (D), the number of species needed to maintain ecosystem function above a set threshold is examined, and used as a metric of ecosystem vulnerability. Figure adapted from Bunker et al. (2005) and Peres et al. (2016).

species needed to retain the 50% ecosystem function by an average of 31.69 species (±19.54 SD). Similar results hold for the other thresholds (Appendix S1), but for simplicity we hereafter only present only results for $S_{T=50}$.

Covariance between response and effect traits had a strong effect on ecosystem vulnerability (Fig. 2). Communities with positive correlations between response and effect traits ($\alpha = 1$) needed an average of 58.14 species ($\pm$ 18.70 SD) to maintain function above the 50% threshold, whereas communities with $\alpha = 0$ needed 14.31 species ($\pm$ 21.13 SD), and those with $\alpha = -1$ needed 7.85 species ($\pm$ 12.24 SD) at the same threshold (Fig. 3, Appendix S1: Figs. S6–S8). Covariation also had a strong impact on compensation outcomes (Fig. 2). While communities with $\alpha = 1$ never

recovered function to the initial level, communities with $\alpha = -1$ always overcompensated, with function commonly surpassing 100% in all replacement scenarios (Fig. 2). In communities with $\alpha = -1$, only 1.14 species ($\pm$ 0.51 SD) were needed to maintain function above the 50% threshold with compensation. Similarly, in communities with $\alpha = 0$, compensation typically caused function to return to initial levels in all compensation scenarios (mean $S_{T=50} = 2.22 \pm 1.98$ SD), but this pattern became increasingly stochastic as more species were lost (Fig. 2, Appendix S1).

The distribution of response and effect traits in the community had a strong effect on ecosystem vulnerability (Figs. 2 and 3). Trait distribution interacted with covariance and compensation to affect the shape of the relationship
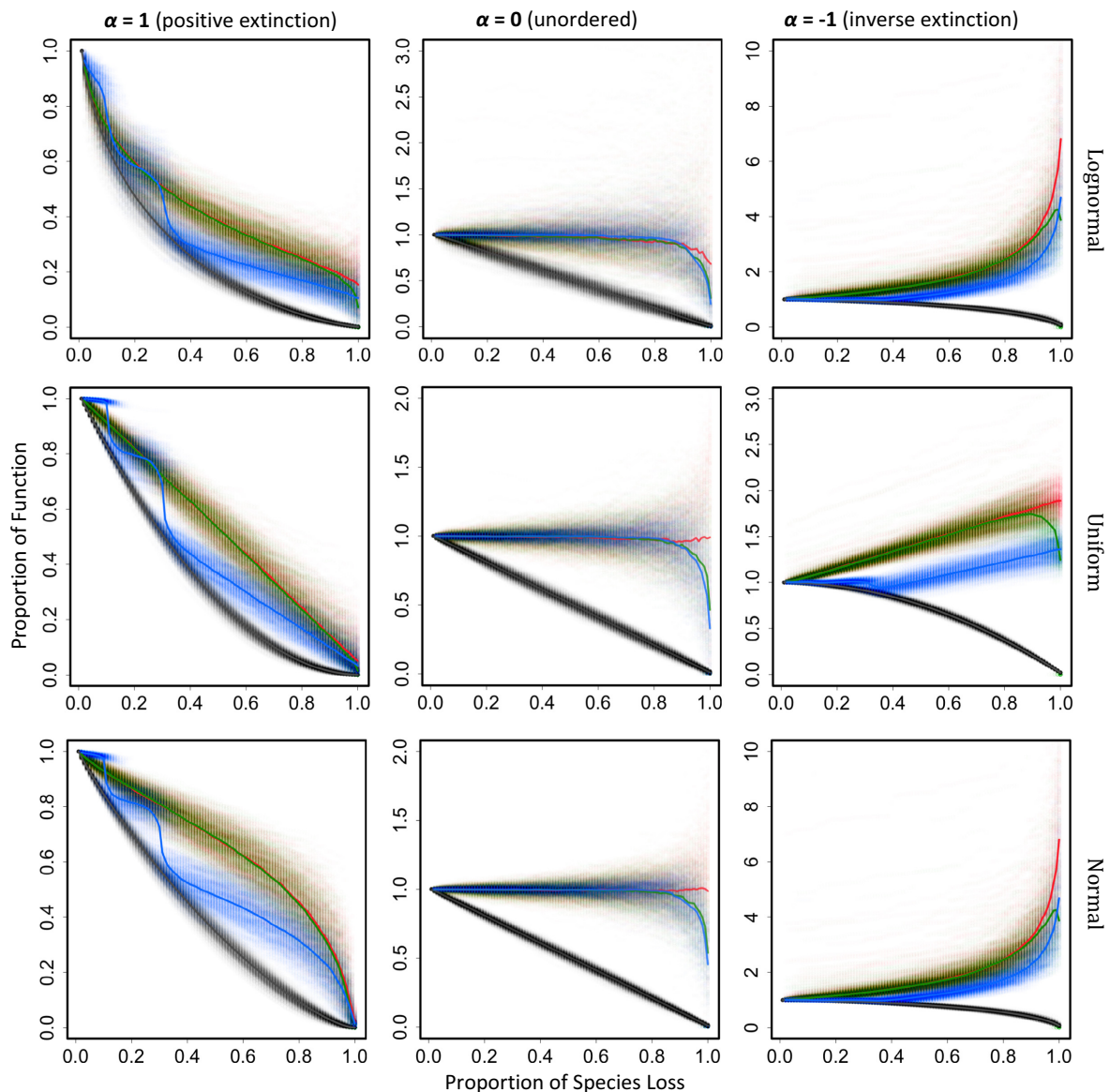

FIG. 2. Effects of response and effect trait covariation and distribution on the relationship between the proportion of species lost and the proportion of initial ecosystem function remaining. Columns are different trait covariation scenarios while rows depict different trait distributions. Each point is a result of one simulation, with colors representing the effects of different compensation scenarios (black: no replacement; red: random replacement; green: uncorrelated trophic-guild replacement; blue: correlated trophic-guild replacement). The lines are the median value of each replacement simulation.

between the proportion of function remaining and the proportion of species lost (Fig. 2). Qualitatively, in communities with $\alpha = 1$, compensation caused the relationship between the proportion of species lost and the proportion of function remaining to be concave up when traits were lognormally distributed, and concave down in communities with normally and uniformly distributed traits (Fig. 2). To maintain function above the 50% threshold $\alpha = 1$ communities in which traits were lognormally distributed required 73.35 species ($\pm$ 9.69 SD), whereas communities in which traits were normally distributed required 43.06 species ($\pm$ 18.93 SD), and communities in which traits were uniformly distributed required 58.01 species ($\pm$ 11.74 SD). In contrast, in communities with $\alpha = -1$, lognormal trait distributions caused higher gains in function than communities with traits normally or uniformly distributed.

Replacement scenarios also had a strong effect on ecosystem vulnerability (Fig. 2). Comparing communities with the same distribution and the same trait covariance structure (i.e., $\alpha = 1$, $\alpha = 0$, $\alpha = -1$) revealed that when trophic position was not correlated with extinction risk, the mitigating effects of compensation were similar to random compensation (Fig. 2). In contrast, when trophic positon was correlated with extinction risk, compensation resulted in more species needed to maintain function in all covariance and distribution scenarios (Figs. 2 and 3).

V_{TOT} and V_{Mean} were both associated with fewer species needed to maintain function across all distributions in communities with positive trait covariation (Fig. 3). In contrast, the higher V_{SD}, the more species were needed to maintain function across all distributions in communities with positive trait variation (Fig. 3). These relationships did not hold for ecosystem functions in communities where $\alpha = 0$ and
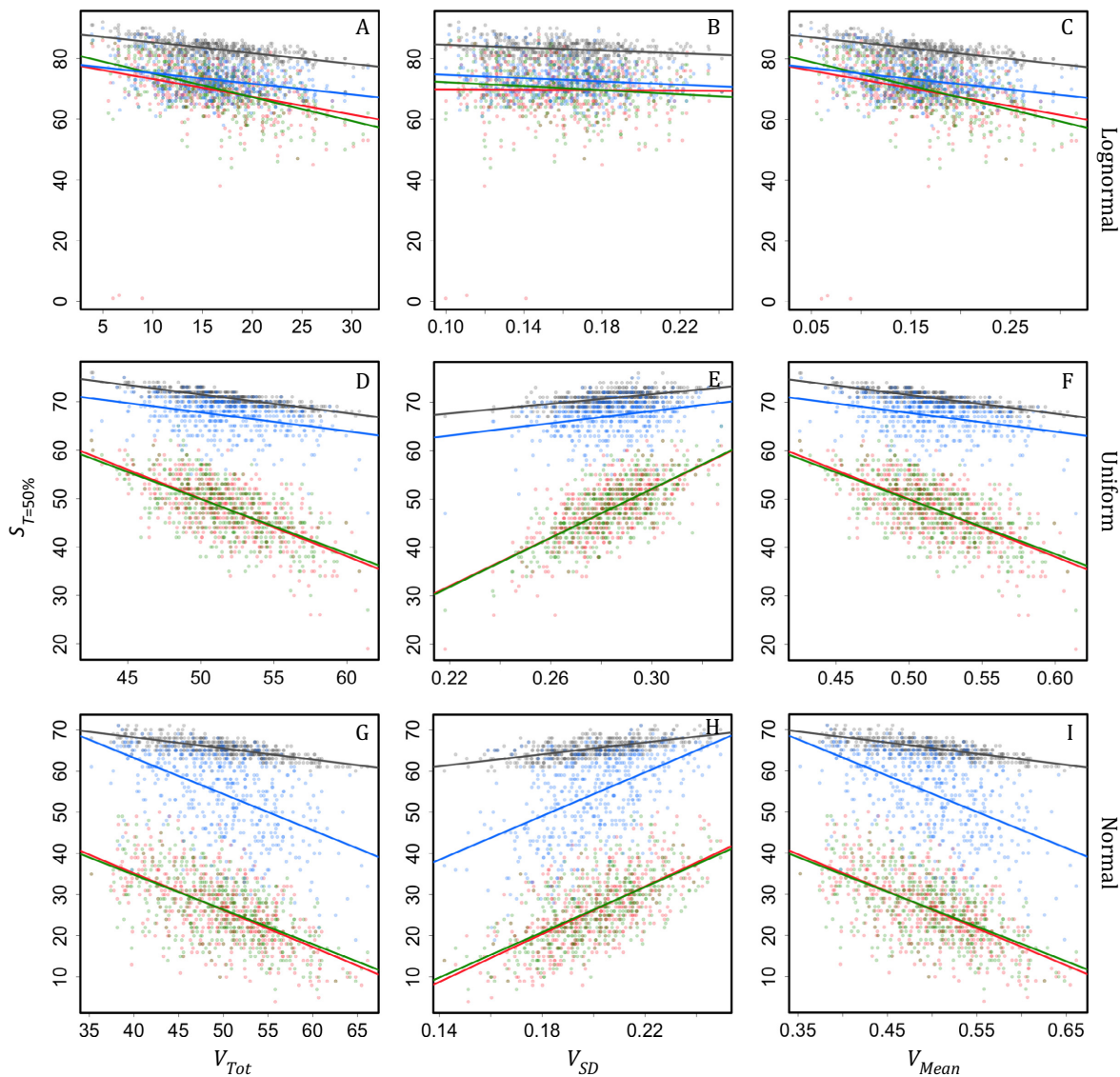

FIG. 3. The effect of trait distribution and compensation on the relationship between initial community vulnerability properties (V_{TOT}: total initial community vulnerability: A, D, G; V_{SD}: initial community trait standard deviation: B, E, H; V_{Mean}: initial mean community vulnerability: C, F, I) and ecosystem vulnerability, measured as the number of species needed to maintain function above 50% of initial ecosystem function. Colors represent different replacement sebastian (as in Fig. 2; see *Methods*).

$\alpha = -1$, since for most of these communities, function usually recovered above all thresholds (Appendix S1).

DISCUSSION

Our study links species traits, community processes and ecosystem properties to identify key factors that determine the vulnerability of ecosystem functions to biodiversity loss. Further, our framework provides a means for assessing when disassembly and compensation will affect the ability of ecosystems to maintain function. We report four major findings. First, despite the role of compensation, the covariance between response and effect traits, which affects the relationship between individual species' probabilities of extinction and their contributions to ecosystem functioning (i.e., V_i and F_i), predicts whether an ecosystem loses or gains function as species are lost. Given the ubiquity of trait trade-offs in animals and plants (Winemiller et al. 2015, Díaz et al. 2016), we expect covariance between response and effect traits to be common features of natural communities. Secondly, trophic structure restricts the degree to which remaining species can compensate for lost species. Consequently, trophic structure increases ecosystem vulnerability when response and effect traits covary positively, and decreases resilience when response and effect traits covary negatively. Thirdly, while some species within communities may compensate for the loss of function associated with community disassembly, the community-scale trait frequency distribution affects the degree to which functional compensation mitigates the impacts of changing composition. Finally, while the positive relationship between functional diversity and ecosystem function is well established, we show that increasing trait variance also increases ecosystem vulnerability when response and effect traits covary positively, a counterintuitive pattern with some empirical support (Weeks et al. 2016). Given current rates of biodiversity change, the need to quantify ecosystem vulnerability has received considerable attention. Our findings suggest identifying relevant response and effect traits, and analyzing their covariation and frequency distribution in multitrophic communities may be key to predicting the ability of ecosystems to maintain function and associated services despite biodiversity loss.

Covariance between response and effect traits was the primary factor affecting whether ecosystems lost or gained function with ongoing disassembly and compensation (Fig. 2). In communities where response and effect traits positively covaried, ecosystems invariably lost function despite the mitigating impacts of compensation. This is because the high effect trait values of the most sensitive species could not be replaced by other species. In ecosystems in which functions are driven by vulnerable species with unique effect traits, changing composition affects ecosystem function, despite the maintenance of biomass through compensation (Solan et al. 2004, McIntyre et al. 2007). In contrast, communities with no covariance between response and effect traits resembled unordered extinctions (Ives and Cardinale 2004). In such cases, function remained relatively unchanged at low levels of extinction. However, as the number of remaining species decreased, the proportion of function remaining tended to become increasingly stochastic since the remaining pool of effect traits was a random sample from the community. Finally, communities with negatively covarying traits tended to experience increases in function with disassembly because the biomass of species with high response trait values (i.e., the most vulnerable) was allocated to species with higher effect trait values, thus increasing total function. While examples of extinction increasing function are less common, the importance of rare species is often attributed to their ability to increase resiliency through compensation (Jain et al. 2014, Leitao et al. 2016). Similarly, invulnerable species can play an insuring role in compensating loss function (Yachi and Loreau 1999). Ultimately, if these rare or invulnerable species have higher effect trait values and can compensate for extinct species, their inclusion in communities should decrease ecosystem vulnerability.

Examining the effects of trait distributions on ecosystem vulnerability leads to two related insights into the role of functionally distinct species and community-level trait variance. First, as the distance in trait space between the most vulnerable and functionally unique species and the rest of the community increases (i.e., where a species falls on the trait frequency distribution), the ability of the remaining community to compensate for the lost species decreases. While this low potential for functional compensation is often attributed to a lack of community redundancy, and is consistent with studies that suggest a positive relationship between ecosystem vulnerability and the presence of unique species (Mouillot et al. 2013, Ricotta et al. 2016), our results suggest that unique species should mainly affect ecosystem vulnerability when that species is also among the most vulnerable. Further, while redundancy is often used as an estimate of ecosystem vulnerability (Ricotta et al. 2016), our results indicate that ecosystem function is particularly sensitive to which traits are considered (response or effect), how they covary with other traits, and the inclusion of outlier species, factors which can be obfuscated by common redundancy metrics. Thus, collecting information on trait distributions and covariance, and evaluating communities using an ecosystem stress test could improve estimates of ecosystem vulnerability.

Second, increased community-level trait variance increases both functional diversity and the vulnerability of ecosystem function. V_{SD} is directly proportional to community functional diversity, and across distributions, the larger V_{SD}, the more species were needed to meet a set threshold of function (Fig. 3, Appendix S1). In contrast, changing composition in communities with low V_{SD} had a smaller influence on ecosystem vulnerability because biomass effects underlay the relationship between biodiversity and ecosystem function. Thus, as trait variance increases in a community, the mitigating effects of compensation decreases. However, when traits covary negatively, variance increases the resiliency of functions in accordance with expected relationships between functional diversity and resiliency (Fig. 2; Oliver et al. 2015). In addition to examining the influence of V_{SD}, we expected to find a positive relationship between V_{TOT}, V_{Mean} and ecosystem vulnerability, but communities with overall higher trait values also had higher trait variance. Although studies quantifying vulnerability properties beyond the species scale are rare, some evidence suggests a positive relationship between biodiversity and total

community vulnerability, which could be mediated by increasing trait variance (Mouillot et al. 2013, Weeks et al. 2016). While we did not explicitly examine the role of species richness in affecting ecosystem vulnerability, increasing functional diversity and trait variance is often associated with increasing ecosystem function and resistance to change due to increasing the diversity of species responses to external drivers (Elmqvist et al. 2003, Laliberté et al. 2010). However, our results suggest that increasing trait variance is also expected to increase the vulnerability of ecosystem functions if response and effect traits covary positively because this reduces the compensatory abilities of species by decreasing redundancy. While this provides a mechanistic explanation, disentangling whether biodiversity jointly increases ecosystem function and ecosystem vulnerability is a paradox that requires further empirical evaluation.

While a large body of work examines the effect of plant biodiversity on ecosystems (Cardinale et al. 2012, Tilman et al. 2014), our multitrophic models suggest that single trophic studies may overestimate ecosystem resiliency and underestimate the vulnerability of ecosystems to biodiversity change in comparison to communities with one trophic level (Fig. 2). In communities where species trophic position was related to response traits, and trait covariation was positive, trophic structure increased ecosystem vulnerability, resulting in abrupt declines in function once the least sensitive species in trophic level went extinct. This suggests that communities in which high effect trait values are unique to a particular trophic level, functional compensation by other trophic levels will be restricted (e.g., long-distance seed dispersal; Peres et al. 2016). Similarly, when response-effect trait covariation was negative, trophic structure decreased the resiliency of functions associated with compensation. In these communities, biomass of the extinct trophic level was not allocated to other trophic levels, restricting the increase in function associated with compensation. In contrast to communities where trophic position was related to extinction probability, communities where trophic position was randomized exhibited a lower ecosystem vulnerability when response and effect traits covaried positively, and higher levels of function achieved when traits covaried negatively. The effects of compensation in these communities were indistinguishable from random compensation, and thus akin to communities with one trophic level. Extensions of work on biodiversity and ecosystem function beyond single trophic levels are rare, but given that trophic position is associated with increased extinction risk (Payne et al. 2016) our results suggest that trophic structure may be an important, but underestimated, contributor to ecosystem vulnerability.

Quantifying ecosystem vulnerability relies on predicting how communities compensate as constituent taxa are lost. The different compensation scenarios we modeled were meant to represent the various replacement rules commonly employed (e.g., Solan et al. 2004, Bunker et al. 2005). However, a few potentially insightful replacement rules were not explored. First, compensation was treated as a zero sum process, so that total community biomass remained constant; however, biomass under- and over-compensation are common, and parameterizing these processes will be important for empirically estimating ecosystem vulnerability in nature (Gonzalez and Loreau 2009). Additionally, species populations can change in biomass, but not go extinct, which could be accommodated in our framework by changing biomass parameters for individual species. Second, our approach considers only mass ratio type effects (sensu Grime 1998), which excludes more complex abundance-function relationships, such as discontinuous traits or traits that do not directly contribute to function. Third, our modeling of trophic structure scenarios represented boundary conditions where either a whole trophic level went extinct, or dissasembly was completely unrelated to trophic positon. While this left out a number of possibilities (e.g., trophic cascades, keystone species, omnivory), the framework is flexible and can be expanded to accommodate more complex compensation scenarios with adequate natural history knowledge of a specific system. Finally, the degree to which biodiversity is decreasing or increasing, is inconclusive (Vellend et al. 2013, Dornelas et al. 2014). While community trait structure varies across spatial and temporal scales, and response traits may also cause some species to increase in abundance, our framework can also accommodate alternative biodiversity change scenarios. Despite these nuances, ecosystem stress tests provide a flexible framework for estimating ecosystem vulnerability that can be easily employed and modified to guide future theoretical, empirical and applied ecological investigations.

Conclusion

While biodiversity may increase the resistance and resilience of ecosystem function (Oliver et al. 2015), our results suggest that this positive effect is conditional on the relationship between trait covariance and distribution. Critically, the vulnerability of an ecosystem's functions, and the services derived from them, is directly related to the community's species composition and functional diversity. At a minimum, how a biota will respond to environmental change and how the altered community may maintain ecosystem function can be predicted with knowledge of (1) the degree to which species can compensate for one another, (2) the degree to which trophic position, response, and effect traits covary, and (3) the frequency distributions of traits in a community. Together, these three factors explain the variety of ecosystem responses to biodiversity change observed in nature. Additionally, by providing an unbiased estimate of ecosystem vulnerability, our methodology can aid conservation and policy in identifying those ecosystem functions and services that might be most vulnerable to novel drivers of change. Ultimately, given that ecosystem vulnerability is directly related to the species found in an ecosystem, changes in biodiversity affect not only the magnitude and variability of ecosystem function but also the sensitivity of ecosystem function to environmental change.

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Supporting Information