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An improved null model for assessing the net effects of multiple stressors on communities

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Abstract

Ecological stressors (i.e., environmental factors outside their normal range of variation) can mediate each other through their interactions, leading to unexpected combined effects on communities. Determining whether the net effect of stressors is ecologically surprising requires comparing their cumulative impact to a null model that represents the linear combination of their individual effects (i.e., an additive expectation). However, we show that standard additive and multiplicative null models that base their predictions on the effects of single stressors on community properties (e.g., species richness or biomass) do not provide this linear expectation, leading to incorrect interpretations of antagonistic and synergistic responses by communities. We present an alternative, the compositional null model, which instead bases its predictions on the effects of stressors on individual species, and then aggregates them to the community level. Simulations demonstrate the improved ability of the compositional null model to accurately provide a linear expectation of the net effect of stressors. We simulate the response of communities to paired stressors that affect species in a purely additive fashion and compare the relative abilities of the compositional null model and two standard community property null models (additive and multiplicative) to predict these linear changes in species richness and community biomass across different combinations (both positive, negative, or opposite) and intensities of stressors. The compositional model predicts the linear effects of multiple stressors under almost all scenarios, allowing for proper classification of net effects, whereas the standard null models do not. Our findings suggest that current estimates of the prevalence of ecological surprises on communities based on community property null models are unreliable, and should be improved by integrating the responses of individual species to the community level as does our compositional null model.

KEYWORDS
additive, antagonistic, community biomass, ecological surprises, environmental change, species richness, synergistic

1 | INTRODUCTION

Understanding the cumulative impacts of environmental changes outside their normal range of variation (i.e., stressors) on biodiversity and ecosystem function is a major challenge for ecology and ecotoxicology (Backhaus, Arrhenius, & Blanck, 2004; Coté, Darling, & Brown, 2016; Lindenmayer, Likens, Krebs, & Hobbs, 2010). Interactions among stressors produce "ecological surprises", whereby their combined effect is not predictable based on their known individual effects, leading to uncertainty in forecasts of the impacts of global change (Christensen et al., 2006; Paine, Tegner, & Johnson, 1998; Sala et al., 2000). However, assessing whether the net effect of stressors constitutes an ecological surprise requires contrasting their realized impact to a null model that captures the linear combination of their individual effects (i.e., additively). Unfortunately, current null models fail to do so, and therefore, provide debatable assessments of the prevalence of ecological surprises in experiments and natural communities (Crain, Kroeker, & Halpern, 2008; Jackson, Loewen, Vinebrooke, & Chimimba, 2016).

Null models are essential to defining the nature of the combined ecological effects of multiple stressors as they provide an expectation of their net effects in the absence of mediating interactions (Folt, Chen, Moore, & Burnaford, 1999). An additive null model assumes that the combined effect of stressors equals the sum of their individual proportional effects, which corresponds to the concentration addition model commonly used in ecotoxicology studies (Backhaus et al., 2004; Loewe & Muischnek, 1926). Statistically significant deviations from the null expectation indicate synergistic (i.e., greater than expected) or antagonistic (i.e., less than expected) net effects of stressors (Coté et al., 2016). Such interactions occur when the presence of one stressor directly alters the intensity of another through physical or chemical alteration (Hooper et al., 2013), a stressor increases or decreases the sensitivity of species to subsequent stressors (Vinebrooke et al., 2004), or through altered interactions among species, such as competition, parasitism, and predation (P. L. Thompson, M. M. MacLennan, & R. D. Vinebrooke, in review; Rosenblatt & Schmitz, 2014; Segner, Schmitt-Jansen, & Sabater, 2014; Kroeker, Kordas, & Harley, 2017).

Here, we show that null models applied to community properties (i.e., based on single stressor effects on species richness or community biomass), do not properly aggregate individual species population responses and therefore, do not accurately predict the linear combination of stressor impacts on whole communities. Such predictions will not reflect the linear combination of population responses to stressors if these are: (i) redundant (Figure 1a), (ii) independently sub-lethal (Figure 1b), or (iii) opposite (Figure 1c). In each of these scenarios, realized change in species richness and community biomass under combined exposure to the stressors will differ from the null expectation based on the individual effects of stressors on that community property, even if species responses are strictly additive. This is a general property of how stressor impacts scale across levels of biological organization (Kroeker et al., 2017), which highlights the need for careful consideration of whether stressor effects are truly nonadditive.

When applied to community-level properties, an additive model cannot account for redundancies in the effects of stressors on populations and "double counts" species extirpations, which can lead to impossible null expectations of >100% loss of species or biomass (Figure 1a). The multiplicative null model is often applied in an effort to circumvent the issue of redundancy between stressor effects as here the net impact of stressors is equal to the product of their individual proportional effects (Coté et al., 2016; Folt et al., 1999). The

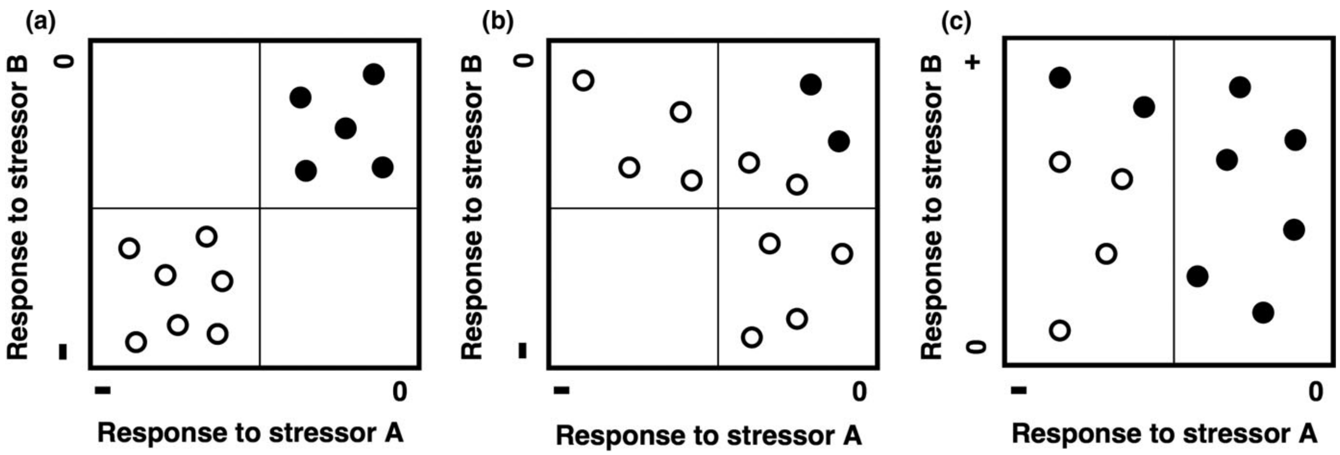

FIGURE 1 Three scenarios in which community property null models fail to predict additive net community responses to paired stressors: redundant effects (a), individual sub-lethal effects exceeding 100% loss in combination (b), and opposing effects (c). In all panels, the thin lines represent the extirpation threshold, beyond which, species are lost when exposed to that stressor alone (left half for stressor A, bottom half for stressor B). The symbols represent the realized combined effect of the stressors on populations (solid = present, open = extirpated) and their positioning shows their relative tolerance of each stressor. Panel a: stressor effects are completely redundant, extirpating the same seven of 12 species. Community property null models overestimate species loss (additive prediction: 116% loss; multiplicative prediction: 83% loss) compared to the actual 58% loss of species. Panel b: individual effects of each stressor are sub-lethal for four of 12 species (upper right quadrat) but two of them cannot persist under exposure to both stressors because the stressors combine to suppress their abundances by more than 100%. Species loss is underestimated (additive prediction: 66% loss; multiplicative prediction: 56% loss) compared to the actual 83% loss. Panel c: the positive stressor B offsets the effects of the negative stressor A, so two species persist under exposure to both stressors that are extirpated by stressor A alone. Species loss is overestimated (additive and multiplicative prediction: 50% loss) compared to the actual 33% loss. In these three cases, using the community property null models leads to the incorrect conclusion of interactive effects of stressors (A—antagonistic, B and C—synergistic) even though the stressors have additive effects on species abundances

multiplicative model corresponds to the independent action model commonly used in ecotoxicology studies (Backhaus et al., 2004; Bliss, 1939). Nonetheless, the multiplicative model is subject to the same errors as the additive model when applied to community properties (Figure 1). Further, when stressors have opposing effects on a response variable, predictions of the multiplicative model are biased toward negative responses. For example, if two stressors have opposite but equal effects, the multiplicative model always predicts that the net effect of the stressors will be negative.

Here, we present a new compositional null model that scales up population-level responses to generate additive null expectations of stressor effects on aggregate community properties. We compare the ability of our compositional model and the standard community property models (i.e., additive and multiplicative) to provide accurate linear predictions of paired stressor effects on species richness and community biomass in simulated communities. We expected that the compositional null model should more often correctly predict the linear combined effect of multiple stressors on species richness and community biomass than either the additive or multiplicative null models applied to community properties.

2 | MATERIALS AND METHODS

We compared the capacity of our compositional null model vs. two null models (additive and multiplicative) based on community-level properties to predict the linear net effects of two stressors on simulated communities. Here, the stressors are noninteractive such that they do not influence the effect of each other and they do not alter the response of species to the other stressor. Further, our simulated community consists of species that do not interact with one another. Therefore, the net effect of the two stressors is the linear combination of each in isolation, and thus can be compared to the predictions of the null models. Our results also extend to scenarios where more than two stressors are present (see Supporting information for case study with three stressors).

We simulated the response of a community to two stressors in R v.3.2.2 (R Development Core Team, 2016) using Lotka-Volterra equations modified from Ives and Cardinale (2004):

$$x_i(t+1) = x_i(t)\exp[r + a_{i,A}m_A(t) + a_{i,B}m_B(t) + bx_i(t)] \quad (1)$$

where $x_i(t)$ is the biomass of species i at time t, r is the intrinsic rate of growth, $a_{i,A}$ and $a_{i,B}$ are the responses of species i to stressors A and B, $m_A(t)$ and $m_B(t)$ are the magnitudes of the stressors at time t, and b is the per-capita rate of intraspecific competition. The result is density-dependent population growth, which is either increased or decreased by the effect of the stressors.

We contrasted four combinations of stressors that varied in their effect on population growth rates: (i) both negative, (ii) one negative, one positive, (iii) both positive, and (iv) a case where species varied in whether they responded negatively or positively to each stressor. We simulated communities consisting of 20 species. The species-specific responses to the two stressors, $a_{i,A}$ and $a_{i,B}$, were drawn from a multivariate uniform distribution [1, 0.3] or [−1, 1] for the mixed scenario, scaled by a factor of 0.005, where the intraspecific correlation between tolerances was determined by ρ. These values were set to be negative or positive, depending on whether the stressor exerted a positive or negative effect. This range of responses ensures that extirpations occur over the range of negative stressors used in the simulations, and that no species can persist at the maximum m for any one negative stressor. We also contrasted three co-tolerance scenarios—no correlation in the responses to each stressor ($\rho = 0$), positive correlation (positive co-tolerance; $\rho = 0.9$), and negative correlation (negative co-tolerance; $\rho = -0.9$).

The populations of each species started at their equilibrium, pre-stress biomass $x_i(t = 1)$. These were determined by the intrinsic rate of growth, r, which for simplicity was set to 0.01 for all species, and the per-capita rate of intraspecific competition, b, which was set to −0.0025. These values were based on those used in Ives and Cardinale (2004). However, our results are robust to relaxing the assumption of equal intrinsic rate of growth and intraspecific competition (Supporting information). We simulated a linear increase in the magnitude, m, of each stressor individually, and both stressors simultaneously, from 0 to 65, over 390,000 time steps. We conducted 100 replicate simulations for each combination of stressor effect and co-tolerance scenario, each time drawing a new set of species-specific responses to the stressors.

We calculated the realized effect of the stressors, individually and in combination, on species richness and community biomass, as the proportional change of the response variable compared to the unstressed community:

$$\Delta R_A = \frac{R_A - R_0}{R_0}, \Delta R_B = \frac{R_B - R_0}{R_0}, \text{ and } \Delta R_{AB} = \frac{R_{AB} - R_0}{R_0} \quad (2)$$

where R_A, R_B, R_{AB} are the values of richness or biomass with each stressor, in isolation (A, B) and in combination (AB). R_0 is the value of richness or biomass in the unstressed community.

We also contrasted the ability of the three null models to predict the realized additive effects of the stressors on species richness and community biomass. We calculated the difference between the predicted and realized changes as $D_{AB} = |\Delta R_{AB}| - \left|\Delta \widehat{R_{AB}}\right|$, where ΔR_{AB} and $\Delta \widehat{R_{AB}}$ are the realized and predicted changes in the response variable with the combined stressors. Positive values of D_{AB} indicate underestimations of ΔR_{AB} and negative values of D_{AB} indicate overestimation of ΔR_{AB}.

2.1 | Compositional null model

Our proposed compositional model predicts the effects of the combined stressors based on the species-specific additive effects of the individual stressors:

$$\hat{x}_{i,\text{multi}} = \max\left(0, x_{i,0} + \sum_j^S (x_{i,j} - x_{i,0})\right) \quad (3)$$

where $\hat{x}_{i,\text{multi}}$ is the predicted biomass of species i with all S stressors combined, $x_{i,0}$ is its biomass in the unstressed community, and $x_{i,j}$ is its biomass with stressor j. In this case, $\hat{x}_{i,\text{multi}}$ is equal to $\hat{x}_{i,\text{AB}}$, and S is equal to 2, for stressors j = A and j = B. Negative values of $\hat{x}_{i,\text{multi}}$ are assumed to be zero. We compared the composition of the predicted community to the unstressed community to calculate the predicted change in species richness and community biomass, $\widehat{\Delta R}_{\text{multi}}$.

2.2 | Additive community property null model

This model predicts the combined effect of the stressors as the sum of the proportional changes in the community response variable of interest:

$$\widehat{\Delta R}_{\text{multi}} = \sum_{j=1}^{S} \Delta R_j, \tag{4}$$

where S is the number of stressors and ΔR_j is the proportional change in the community response variable when exposed to stressor j. Although not intrinsic in the null model, we limited the expected response to -1 because it is unrealistic for a community to lose more than 100% of its species or biomass.

2.3 | Multiplicative community property null model

This model predicts the effect of the combined stressors as:

$$\widehat{\Delta R}_{\text{multi}} = \left(\prod_{j=1}^{S} 1 + \Delta R_j\right) - 1. \tag{5}$$

This equation is reformulated from the independent action model (Bliss, 1939) and the multiplicative model (Folt et al., 1999) to allow for both positive and negative effects of the stressors. Like the other null models used here, negative and positive values represent decreases and increases in community properties respectively.

3 | RESULTS

3.1 | Species richness

The compositional null model predictions match the realized species loss, except when the stressors have opposing effects and the negative stressor is strong enough to cause extirpations when applied without the positive stressor (Figure 2). In contrast, the two community property models do not consistently predict the net effects of the stressors in any scenario, except when stressors are both positive. Discrepancies between predicted and realized species loss in the compositional model occur because the model predictions are based on the effect of the individual stressors on the biomass of each species. Therefore, the negative predicted effect of a stressor on a species cannot exceed its biomass in the unstressed community, but the positive effect of a stressor has no limit. If a species is more sensitive to the negative than positive stressor, it will be lost from the community, but at a higher level of exposure than with the negative stressor alone. The compositional model fails to accurately predict the combined effect of stressors in this case because the predicted effect of the positive stressor continues to increase with higher stressor magnitude, while the predicted effect of the negative stressor remains constant (Figure 3). Here, the compositional model underestimates species loss, but its predicted species losses are closer to the realized effects than those based on the community property null models.

The community property null models underestimate species loss when both stressors are negative or when species have mixed responses to the stressors and stressor magnitude is low (Figure 2). Here, species losses are underestimated because the models fail to predict cases when species can persist with either stressor in isolation, but not together (Figure 1b). In contrast, the community property null models overestimate species loss when stressors have opposing effects or when species have mixed responses to the stressors and stressor magnitude is high. In these scenarios, the models fail to predict cases when positive responses to stressors rescue species from the effects of negative stressors, which would otherwise cause their extirpation (Figure 1c). The correlation of species responses to the stressors alters the magnitude of species loss at any given stressor level, but this had little effect on the performance of the null model predictions (Figure 2).

3.2 | Community biomass

Like the species richness metric, the compositional null model predictions match the realized changes in community biomass except when both stressors exert large and opposing effects, and the negative stressor is strong enough to cause extirpations in isolation (Figure 4). The additive community property null model accurately predicts changes in biomass when both stressors are positive and when stressors, in isolation or combination, do not cause extirpations. However, realized changes in biomass deviate from predicted changes based on the additive model when high magnitudes of negative stressors cause species to be lost from the community (Figure 4). When the cumulative effect of negative stressors cause biomass loss to exceed 100% for a given species, biomass losses are "double counted" and thus overestimated by the additive community property model (Figure 1a). Similar to the compositional model, when stressors have opposing effects on species and the negative stressor is strong enough to cause extirpations in isolation, the additive community property null model erroneously predicts biomass growth because the predicted effect of the negative stressor is bounded, while that of the positive stressor is not (see description for compositional diversity predictions, Figure 3). When species have mixed responses to the stressors, the additive community property null model underestimates biomass increases when species responses to the stressors are positively correlated, overestimates biomass increases when responses are negatively correlated, and switches from under- to overestimating increases in biomass as the magnitude of the stressors increases when responses are not correlated. These patterns are driven by the combined effects of "double

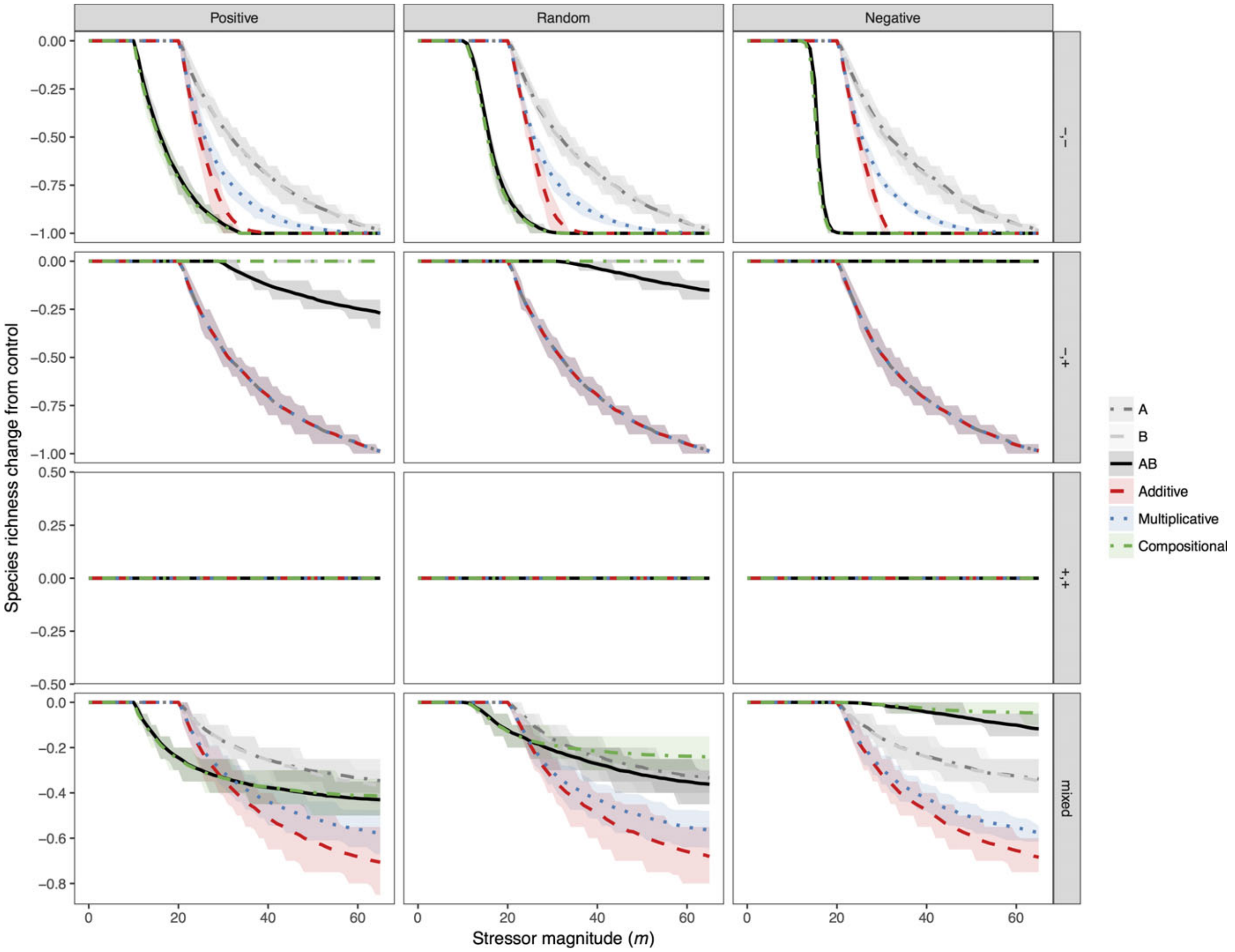

FIGURE 2 Simulated species richness change in response to increasing stressor magnitude. Gray lines show the individual effects of stressors A and B while black lines indicate the combined impact of the stressors (AB). Red and blue lines depict the additive and multiplicative null predictions, while green lines show the compositional null model predictions. Each panel column indicates a different co-tolerance scenario (negative—left, random—middle, positive—right). Each panel row shows a different stressor combination (negative, negative—top; negative, positive—top middle; positive, positive—lower middle; mixed—bottom). Lines and shaded bands indicate the mean and interquartile range across 100 replicate simulations

counting" biomass loss, and the bounded effects of negative responses to stressors.

Predictions based on the multiplicative community property null model always deviate from the realized changes in community biomass (Figure 4). When species responses to both stressors are negative, the model underestimates the cumulative loss of biomass because biomass losses are additive at the species level. The model also erroneously predicts biomass loss when two stressors have opposing effects, despite there being either no net change or increases in actual biomass. This occurs because the stressors offset each other at the community level, but their product is negative, which, when added to the additive effect, results in a prediction of biomass loss. The model overestimates biomass gains when both stressors have positive effects because the positive product is added to the additive effect. When species have mixed responses to the stressors, the model underestimates biomass increases when species responses to the stressors are positively correlated, overestimates biomass increases when responses are negatively correlated, and switches from under- to overestimating biomass increases as stressor magnitude increases when responses are not correlated. The correlation of species responses to the stressors alters the magnitude of biomass change at any given stressor level, but has no consistent effect on the performance of the null model predictions (Figure 4).

4 | DISCUSSION

Concluding whether the effects of multiple stressors are additive, antagonistic, or synergistic requires comparison to a null model that accurately captures the linear combination of the independent effects of each stressor (Folt et al., 1999; Griffen, Belgrad, Cannizzo,

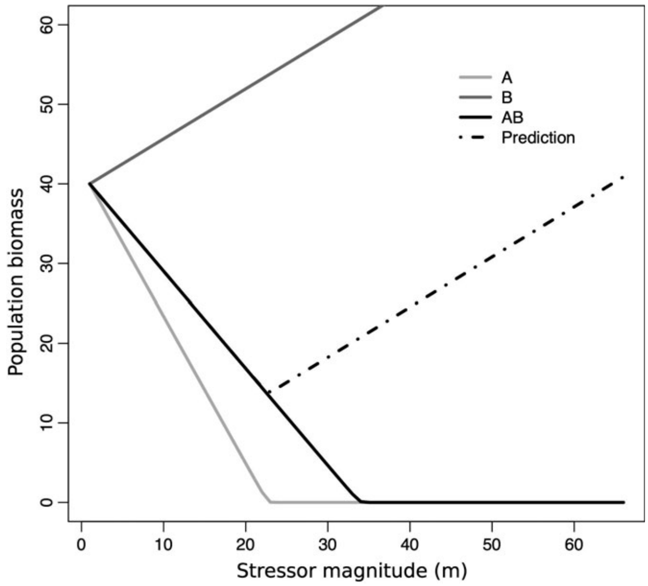

FIGURE 3 Illustration of why the compositional null model fails to predict the net impact of a positive and a negative stressor at high stressor magnitude. Solid lines show the realized biomass of a species under each single stressor (gray), and the combined stressors (black). The compositional model prediction (dashed black) matches the realized biomass below the stressor magnitude that causes the species to be lost in response to the negative stressor. At higher stressor magnitude, the compositional model underestimates biomass loss because the predicted effect of the negative stressor is bounded

Knotts, & Hancock, 2016). Our simulations demonstrate that community property models (additive and multiplicative) fail to meet this requirement. These models can under- or overestimate the net effect of multiple stressors, depending on the types of stressors and the community property of interest. In contrast, our new compositional model, based on species-specific responses to the stressors, accurately predicts the linear combination of multiple stressors on both community diversity and biomass in most scenarios. Therefore, applying our compositional model should lead to more appropriate conclusions of whether stressors have interactive effects on ecological communities.

Our compositional model provides accurate linear predictions of the net effect of stressors because it is based on the direct effects of stressors on individual species within a community (Sibly & Hone, 2002). Unlike community property null models based on aggregate community-level properties, the accuracy of predictions of the compositional model is unaffected by cases in which: (i) the sum of the individual effects of the stressors exceeds 100% loss of species abundance, (ii) species persist when exposed to either stressor in isolation, but are extirpated under combined exposure to the stressors, and (iii) species respond positively to one stressor but negatively to the other (Figure 1). Because community property null models are unable to provide correct linear predictions in these cases, conclusions of the net effect of stressors based on their null expectations may be erroneous.

In addition, the accuracy of predictions of our compositional model, unlike community property models, is not affected by the pattern of species co-tolerance to the stressors. The pattern of co-tolerance determines the degree to which the effects of stressors are redundant and therefore, the likelihood that the sum of the individual effects of stressors on a species will exceed 100% (Darling, McClanahan, & Coté, 2013; Vinebrooke et al., 2004). The compositional model accounts for redundant effects of stressors because its predictions are based on species-specific responses to the stressors and therefore, does not allow greater than 100% loss of species abundances. In contrast, community property models based on aggregate properties are unable to separate effects of stressors on individual species and are liable to erroneously “double count” species extirpations when stressors have redundant effects.

The only scenario in which our compositional model does not accurately predict the linear combination of stressors is when the stressors have opposing effects on the species, and the negative stressor in isolation is strong enough to extirpate species. Here, the predicted effect of the negative stressor on a species cannot exceed its biomass in the unstressed community, but the predicted effect of the positive stressor is unlimited. Therefore, beyond the stressor magnitude at which the negative stressor extirpates a species, the predicted effect of the negative stressor remains constant, while the predicted effect of the positive stressor continues to increase. Because null expectations of the compositional model are based on the sum of the individual effects of the stressors on species, the effect of the positive stressor is predicted to outweigh the effect of the negative stressor. However, if a species is more sensitive to the negative vs. positive stressor, it will be lost from the community, but at a higher stressor magnitude than when exposed to the negative stressor alone. Consequently, caution should be used when drawing conclusions on the net effects of stressors whenever a positive stressor is paired with a negative stressor, which would independently cause species to be lost from the community. In these situations, our compositional null model will always underestimate species and biomass loss.

Community property null models do not provide accurate linear predictions of stressor effects in most cases and can lead to spurious conclusions of stressor interactions even when stressors combine linearly. In contrast, net effects of stressors that deviate from null expectations of the compositional model signal true stressor interactions, whereby one stressor modifies the response of the community to another. Such deviations may occur when one stressor alters the magnitude of another stressor, exposure to one stressor alters the tolerance of species to another stressor, or interspecific interactions modify the response of species to the stressors (Crain et al., 2008; Griffen et al., 2016; Schuwirth, Dietzel, & Reichert, 2016; Segner et al., 2014). By consistently providing linear null expectations of the combined effect of stressors, the compositional model enables correct classifications of the net effects of stressors as additive, synergistic, or antagonistic. Therefore, use of the compositional null model will allow us to identify stressor combinations that impact

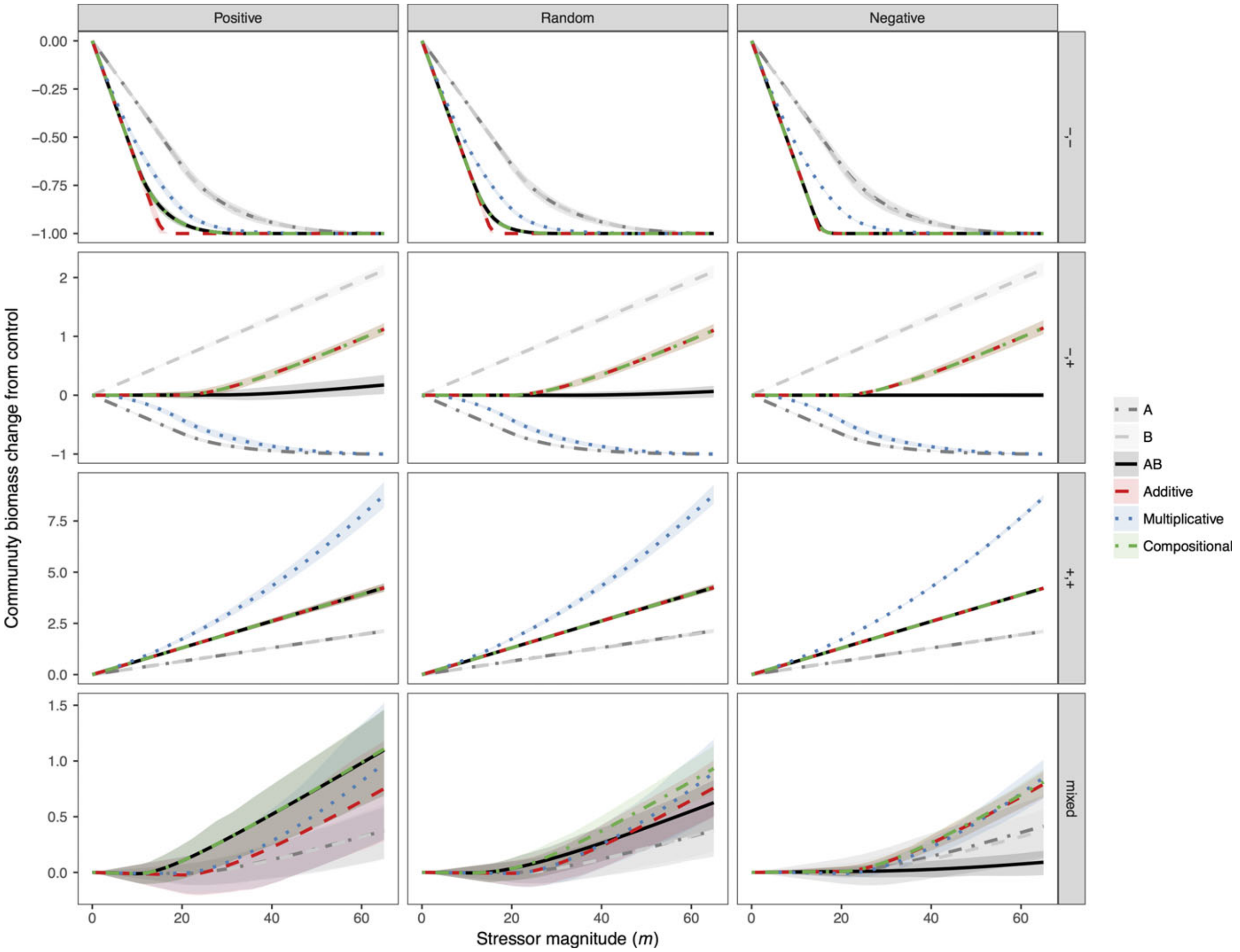

FIGURE 4 Simulated community biomass change in response to increasing stressor magnitude. See Figure 2 caption for details

communities in nonlinear and ecologically meaningful ways (Coté et al., 2016; Griffen et al., 2016).

To date, meta-analyses of multiple stressor effects have been based on community property null models, calling into question their conclusions on the frequency of stressor interactions (Crain et al., 2008; Jackson et al., 2016). Although it is unclear how much the conclusions from these studies would differ if they were based on compositional null model predictions, it is likely that the prevalence of antagonistic, additive, and synergistic responses would change. For example, the reported predominance of antagonistic effects of stressors on communities (Crain et al., 2008; Jackson et al., 2016) may be confounded by the inability of community property null models to account for redundancies in stressor effects. In particular, the additive null model, when applied to community-level properties is biased toward antagonistic responses whenever species co-tolerances are not completely negative. If the reported prevalence of antagonistic responses at the community-level is indeed due to the use of inaccurate null models, the use of the compositional null model may reveal greater overall net effects of stressors on communities with higher frequencies of additive and synergistic net effects, following population-level trends (Crain et al., 2008; Jackson et al., 2016). It should, however, be noted that this issue does not extend to meta-analyses performed on population properties (Darling & Coté, 2008).

The key feature of our compositional null model is that it calculates stressor effects at the individual population levels and aggregates these to determine the expected effects at the community level. In our simulations, we have assumed that stressors have additive effects at the population level. However, our compositional null model can be adapted to incorporate any of the null models that have been proposed in the fields of ecology, ecotoxicology, and pharmacology for assessing the net effects of stressors, toxins, and drugs in combination (Bliss, 1939; Folt et al., 1999; Liess, Foit, Knillmann, Schäfer, & Liess, 2016; Loewe & Muischnek, 1926). For example, if stressors are hypothesized to have multiplicative impacts (Folt et al., 1999), this can be done by calculating the expected multiplicative effect of the stressors on each individual species, then scaling these effects up to the community-level properties. In this way, we can ask whether stressors combine to have unexpected impacts on community-level properties based on these null expectations.

Although we have shown the ability of the compositional null model to provide linear predictions using two stressors, the accuracy of its predictions is robust to additional stressors (Fig. S1). In contrast, errors in linear predictions associated with community property null models should become more pronounced with additional stressors. Of course, it is likely that interactions among stressors should increase with the number of concurrent stressors (Coté et al., 2016), leading to greater deviations from the linear prediction; however, only the compositional model will enable us to correctly identify these interactions.

Applying our compositional null model to empirical data requires that we modify our statistical methods to determine whether the observed net effect of stressors differs from our expectation. Whereas statistical methods exist for applying the additive and multiplicative community property null models to observational data (Crain et al., 2008; Gurevitch, Morrison, & Hedges, 2000; Jackson et al., 2016), applying the compositional null model is less straightforward. In this case, we suggest a bootstrap method could be used to estimate an effect size and confidence interval by resampling the experimental replicates used to estimate D_{AB} (Efron & Tibshirani, 1993).

Overall, our compositional null model provides accurate predictions of the linear combinations of multiple stressors on ecological communities while current null models based on aggregate community-level properties fail to do so. Although, the compositional model has limitations when positive and negative stressors combine, it represents a substantial improvement over current models across a range of stressor types and patterns of species co-tolerance. We argue that correct classifications of stressor effects on communities as additive, antagonistic, or synergistic require use of the compositional model, suggesting that estimates of the prevalence of stressor interactions on communities based on current null models are unreliable. Nonetheless, use of the compositional null model in future studies and the potential re-analysis of previous studies will allow correct interpretations of net effects of stressors on communities—information that will be essential for anticipating, predicting, and managing global change (McGill, Dornelas, Gotelli, & Magurran, 2015; Waters et al., 2016).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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