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Broadly inflicted stressors can cause ecosystem thinning

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Abstract
Many anthropogenic stressors broadly inflict mortality or reduce fecundity, including habitat destruction, pollution, climate change, invasive species, and multispecies harvesting. Here, we show—in four analytical models of interspecies competition—that broadly inflicted stressors disproportionately cause competitive exclusions within groups of ecologically similar species. As a result, we predict that ecosystems become progressively *thinner*—that is, they have progressively less functional redundancy—as broadly inflicted stressors become progressively more intense. This may negatively affect the temporal stability of ecosystem functions, but it also buffers ecosystem productivity against stress by favoring species less sensitive to the stressors. Our main result follows from the weak limiting similarity principle: species with more similar ecological niches compete more strongly, and their coexistence can be upset by smaller perturbations. We show that stressors can cause indirect competitive exclusions at much lower stressor intensity than needed to directly cause species extinction, consistent with the finding of empirical studies that species interactions are often the proximal drivers of local extinctions. The excluded species are more sensitive to the stressor relative to their ecologically similar competitors. Moreover, broadly inflicted stressors may cause hydra effects—where higher stressor intensity results in higher abundance for a species with lower sensitivity to the stressor than its competitors. Correlations between stressor impacts and ecological niches reduce the potential for indirect competitive exclusions, but they consequently also reduce the buffering effect of ecosystem thinning on ecosystem productivity. Our findings suggest that ecosystems experiencing stress may continue to provision ecosystem services but lose functional redundancy and stability.

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Introduction

Broadly inflicted stressors are processes that simultaneously cause increases in the rates of mortality, or decreases in the rates of fecundity, for many species in an ecosystem. Many broadly inflicted stressors are anthropogenic—such as habitat destruction, degradation and fragmentation, nutrient pollution, pollution via release of pesticides, industrial chemicals and other toxins, climate change, multispecies harvesting, and some invasive species, among others.

The potential ecological consequences of broadly inflicted stressors are important to understanding and managing the ecology of the Anthropocene. Broadly inflicted anthropogenic stressors cause enough direct mortality (or decreased fecundity, e.g., DDT) to be some of the most significant threats to biodiversity (Maxwell et al. 2016). Indirect impacts of anthropogenic stressors also cause substantial mortality via species interactions and other ecosystem processes [e.g., nutrient loading affecting competition or food chains (see Schindler 2006 and Harpole and Tilman 2007) or climate change changing patterns of species co-occurrence (see Urban et al. 2016 and Pecl et al.

2017)]. These indirect effects are often less well understood, but they may be a greater driver of local extinction than direct mortality (Cahill et al. 2012; Ockendon et al. 2014).

Here, we examine indirect ecological effects of broadly inflicted stressors, mediated by interspecies competition. We specifically focus on the interaction between broadly inflicted stressors and weak limiting similarity (Abrams 1983). *Weak limiting similarity* describes the phenomenon whereby, as the ecological similarity between two species increases, the suite of environmental conditions that could allow competitive coexistence shrinks, which means that smaller environmental changes or perturbations could lead to the competitive displacement of a species (Vandermeer 1975; Abrams 1983).

Weak limiting similarity follows from the well-known principle that species with more similar ecological niches compete more strongly with one another. This principle—originated in various forms by Darwin (1859), Gause (1934), Hutchinson (1959), and Hardin (1960)—is highly intuitive. Two consumers that specialize on the same resource will compete more strongly with each other than will consumers specializing on different resources. Two prey species sharing a predator will indirectly compete (Holt 1977) more than will two prey species having different predators. In classic ecological theory, two species competing for a single limiting resource cannot coexist, because whichever of the two can survive on the lowest resource abundance can outcompete the other (Hardin 1960; Tilman 1980).

Weak limiting similarity has been shown to be highly theoretically general (Meszéna et al. 2006; Barabás et al. 2014; Pásztor et al. 2016), and it has also been empirically validated (e.g. Stubbs and Wilson 2004; Violle et al. 2011; see also reviews by Schluter 2000 and Cavender-Bares et al. 2009). [*Strong limiting similarity* would, in contrast, imply that species more similar than a certain threshold could not coexist under any circumstances, and is a less general phenomenon (Abrams 1983)]. Indeed, the principle of weak limiting similarity applies to competition for multiple resources (e.g., MacArthur and Levins 1967), tradeoffs between competition and colonization (e.g., Tilman 1994; Kinzig et al. 1999), tradeoffs between high-abundance and low-abundance resource specialization (e.g., Armstrong and McGehee 1980), and temporal niches (e.g., Chesson and Warner 1981; Loreau 1989, 1992). Meszéna et al. (2006) show that weak limiting similarity and the competitive exclusion principle apply highly generally, where ecological similarity is defined as similarity in either species' impacts on, or the degrees to which they are impacted by, the regulating variables of their environment (e.g., resources, predators, or abiotic factors).

We show that, as a result of weak limiting similarity, broadly inflicted stressors can change coexistence into competitive displacement especially easily among groups of ecologically similar species. Unless stressors affect all competing species identically, increasing the intensity of a stressor will perturb species' relative competitive abilities. (Ecologically similar species may have markedly different sensitivities to broadly inflicted stressors, e.g., because of differing population growth rates, mortality rates, etc.) Weak limiting similarity ensures that smaller perturbations—and thus lower-intensity stressors—are needed, on average, to upset the coexistence of more ecologically similar pairs of species. Consequently, increasing the intensity of a stressor (i.e., the magnitude of mortality or reduced fecundity it inflicts) causes extinctions disproportionately within groups of ecologically similar species. This results in a pattern we call "ecosystem thinning": decreases in the number of functionally similar species—and thus loss of functional redundancy—as the intensity of stressors increases. Ecosystem thinning has several important implications for ecosystem function, which we discuss.

Our main analysis uses a simple model of Lotka-Volterra-type competition, inspired by the models of MacArthur and Levins (1967), Pianka (1974), and Vandermeer (1975). In the Appendix, we show that the key prediction underlying our secondary results—that increasing ecological similarity among species reduces the intensity of a broadly inflicted stressor needed, on average, to change coexistence into competitive displacement—is robust in three qualitatively different mechanistic models of two-species competition. These models include a model of resource competition (following Tilman 1980), a model of resource competition and apparent competition (following Holt et al. 1994), and a model of competition-colonization tradeoffs (following Calcagno et al. 2006). We focus our analysis on equilibrium statics of communities of species that would coexist in the absence of one or more stressors. Thus, we do not explicitly consider stressor-mediated invasions, transient dynamics, or stochastic forces, but we discuss how these factors might impact our results.

Weak limiting similarity and broadly inflicted stress

We assume there is an initial community of I coexisting species. Using Vandermeer's (1975) notation, we assume that each species' per-capita growth rate in abundance (N_i denotes the abundance of species i) has a maximum, r_i for species i, and declines according to linear competition and density dependence terms (a_{ij} denotes the per-capita effect of species j on the per-capita growth of species i). There is a stressor having intensity (E), and species i suffers per-capita mortality (or loss of fecundity) ($r_i v_i E$) from it. Here, v_i represents the sensitivity of species i to the stressor—its per-capita, per-unit-intensity mortality rate, as a fraction of its maximum growth rate (analogous to Burgess et al.'s 2013 "vulnerability" concept; Holt 1977 also invokes a similar concept in the context of apparent competition). The per-capita rate of change in abundance of species i is thus given by

$$\frac{dN_i}{N_i dt} = r_i(1-v_i E) - \sum_{j=1}^{I} a_{ij} N_j. \tag{1}$$

In the summation term, a_{ii} represents the strength of density dependence on species i, and a_{ij} represents the strength of competition from species j on species i (when $j \neq i$). Following Pianka (1974), we measure niche similarity (denoted o_{ij} or o_{ji} for species i and j) as the strength of interspecies competition relative to intraspecies competition

$$o_{ij} = o_{ji} = \sqrt{\frac{a_{ij} a_{ji}}{a_{ii} a_{jj}}}. \tag{2}$$

Note that, while we define niche similarity to be symmetric ($o_{ij} = o_{ji}$), competition need not be (i.e., $a_{ij} \neq a_{ji}$, typically).

Weak limiting similarity

In the section on ecosystem thinning below, we will relate this niche similarity concept explicitly to overlap in resource utilization along a cardinal (i.e., numeric and continuous) niche axis, following MacArthur and Levins (1967) (Fig. 1a). However, these additional complexities are not necessary to demonstrate weak limiting similarity and how it makes the

coexistence between more ecologically similar pairs of species (i.e., pairs i and j having high o_{ij}) disrupted by lower-intensity (E) stress (see also Meszéna et al. 2006).

A group of species will stably coexist if each can increase in abundance when it is rare and the other species are at equilibrium (the mutual-invasibility criterion; see Chesson 2000). With only two species in the community—denoted with subscripts 1 and 2, Vandermeer (1975) showed that stable coexistence requires Eq. (3a) to hold without stress (i.e., when $E = 0$) (see also Chesson 2000 and Letten et al. 2017 for similar results). With stress (i.e., when $E > 0$), it is easy [from Eq. (1)] to derive an analogous coexistence [Eq. (3b)]

$$\frac{a_{21}}{a_{11}} < \frac{r_2}{r_1} < \frac{a_{22}}{a_{12}}. \tag{3a}$$

$$\frac{a_{21}}{a_{11}} < \frac{r_2(1-v_2 E)}{r_1(1-v_1 E)} < \frac{a_{22}}{a_{12}}. \tag{3b}$$

From Eqs. (2) and (3a), the ratio between the upper bound and lower bound of $\frac{r_2}{r_1}$ allowing coexistence, without stress, is $\frac{1}{o_{12}^2}$. This implies that when there is little niche similarity ($o_{12} \ll 1$), there is a large range of relative maximum growth rates that allows coexistence. However, if the two species have
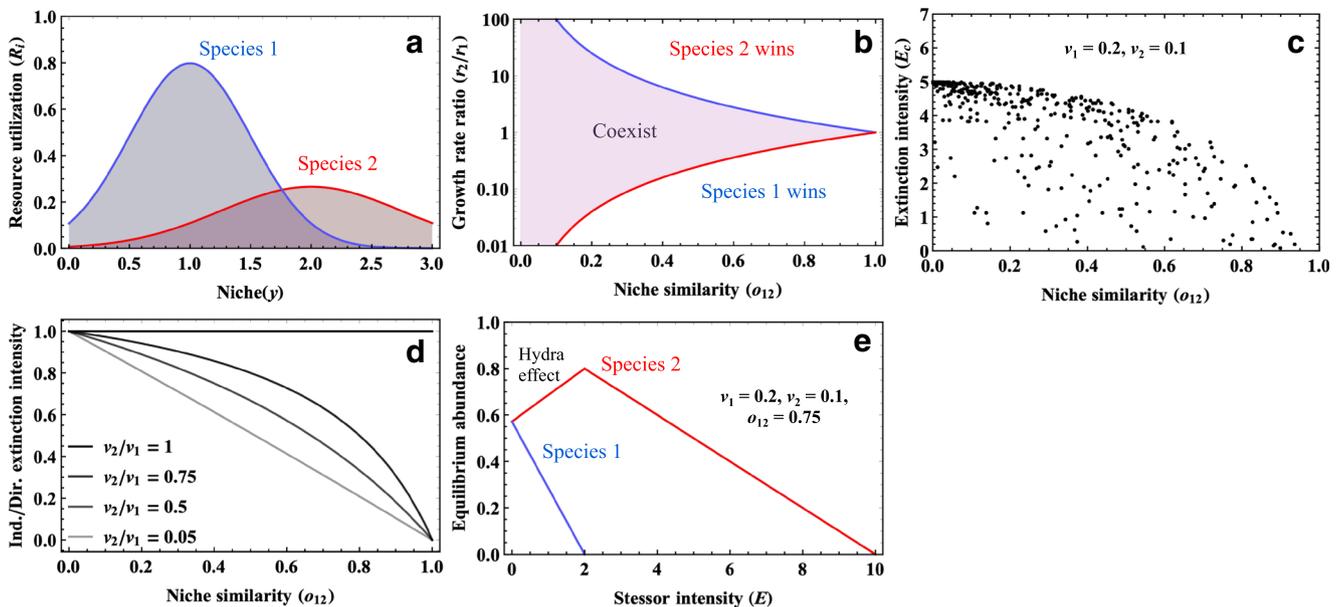

Fig. 1 Ecological similarity and the narrowing coexistence window in a two-species model. **a** Two hypothetical resource-utilization functions, from which niche similarity and competition coefficients can be calculated, following MacArthur and Levins (1967) and Pianka (1974). **b** [From coexistence Eq.(3a)] how the range of relative species growth rates (r_2/r_1) allowing coexistence becomes progressively smaller as niche similarity (o_{12}) increases ($a_{11} = a_{22} = 1$, in the example shown). **c** How the average and upper limit of stressor intensities causing competitive exclusion of the more sensitive competitor decrease as niche similarity (o_{12}) increases. Each point represents a random draw from parameter distributions ($n = 1000$; r_1, $r_2 \sim U[0.5, 2.5]$; y_1, $y_2 \sim U[0, 2]$; w_1, $w_2 \sim U[0, 1]$; K_1, $K_2 \sim U[0.5, 2]$; a_{ij} parameters are calculated from

Eq. (11)), filtered to only include pairs of species that coexist without stress. **d** How increasing niche similarity (o_{12}) and increasing disparity in sensitivity (v_2/v_1) decrease the stressor intensity needed to indirectly cause extinction via competition, as a fraction of the intensity needed to directly cause extinction, to the more sensitive competitor. **e** How the less-sensitive competitor can initially experience a hydra effect (increasing abundance as stressor intensity increases), due to the indirect benefit of stress via reduced competition being greater than the direct effect of mortality or reduced fecundity from stress. In **c** and **d**, $\frac{r_1 a_{21}}{r_2 a_{11}} = \frac{r_2 a_{12}}{r_1 a_{22}}$, and other parameter values are indicated

identical niches ($o_{12} = 1$), the species can only coexist at a single ratio of maximum growth rates (Fig. 1b). Thus, the coexistence of ecologically similar species is sensitive to perturbation. This is weak limiting similarity.

Greater ecological similarity, less stress needed to disrupt coexistence, on average

With identical sensitivities to stress (i.e., $v_1 = v_2$), Eqs. (3a) and (3b) become equivalent and the stressor's intensity has no effect on coexistence. However, if the two species have different sensitivities to the stressor, increasing the intensity of the stressor (E) increases $\frac{r_2(1-v_2E)}{r_1(1-v_1E)}$ if $v_1 > v_2$ (or decreases this ratio if $v_1 < v_2$). Thus, any intensity of stress (i.e., any $E > 0$) will disrupt the coexistence of a pair of species with identical niches ($o_{12} = 1$) and differing sensitivities. For pairs of species with non-identical niches ($o_{12} < 1$), the intensity of the stressor needed to cause the competitive exclusion of the more sensitive competitor (that with higher v_i) will depend on where their ratio of maximum growth rates ($\frac{r_2}{r_1}$) falls within the unstressed coexistence range [Eq. (3a)]. However, the critical stressor intensity (E_c), causing competitive exclusion of the more sensitive competitor (i) ($v_i > v_j$), will be bounded by (assuming stable coexistence without stress)

$$0 < E_c \leq \frac{\left(1-o_{ij}^2\right)}{v_j\left(\frac{v_i}{v_j}-o_{ij}^2\right)}. \tag{4}$$

Here, the upper bound is defined by the scenario in which the less-sensitive competitor (j) was barely able to coexist without stress ($\frac{a_{ji}}{a_{ii}} = \frac{r_j}{r_i}$); the lower bound (0) is defined by the scenario in which the more-sensitive competitor (i) was barely able to coexist without stress ($\frac{a_{ij}}{a_{jj}} = \frac{r_i}{r_j}$, and thus, any stress at all will upset coexistence).

The upper bound of E_c approaches zero as o_{ij} approaches 1, while the lower bound is always zero. Thus, both the maximum critical stressor intensity and the average critical stressor intensity across pairs of coexisting species assembled from randomly chosen parameter values will decrease as niche similarity increases (Fig. 1c). This implies that coexistence will be disrupted at lower stressor intensities among pairs of ecologically similar species, relative to pairs of ecologically dissimilar species, on average. The upper bound of E_c also shrinks as v_i/v_j increases. Thus, the stressor intensity causing competitive exclusion is lowest among species which are both ecologically similar, and differing in their sensitivities to stress. This is the principle upon which the concept of ecosystem thinning rests, and we demonstrate the robustness of this principle in three qualitatively different mechanistic two-species competition models in the Appendix (see Fig. 3).

Stressor intensities needed for indirect vs. direct exclusion of more sensitive competitors

With no competition, species i's population dynamics are given by

$$\frac{dN_i}{N_i dt} = r_i(1-v_iE)-a_{ii}N_i \tag{5}$$

and the stressor intensity needed to cause extinction of species i, denoted $E_{c,i}$, is

$$E_{c,i} = \frac{1}{v_i}. \tag{6}$$

With two-species competition, the largest possible stressor intensity required to competitively exclude the more sensitive competitor i [the upper bound of E_c from Eq. (4)] is equal to $1/v_i$ when there is no niche similarity ($o_{ij} = 0$), strictly less than $1/v_i$ when there is niche similarity ($o_{ij} > 0$, and $v_i > v_j$), and approaches zero as o_{ij} approaches 1. Thus, our theory predicts broadly inflicted stressors cause competitive exclusions, among ecologically similar species, at much lower intensities than would be required to directly cause extinction. This pattern is most pronounced when the species have large differences in sensitivity (Fig. 1d).

Hydra effects among less-sensitive competitors

As shown above, broadly inflicted stressors can drive relatively more sensitive competitors to extinction. We also find that, in some cases, they may cause increases in abundance of relatively less-sensitive competitors—a phenomenon known as the "hydra effect" (Abrams 2009). The hydra effect occurs, in these cases, because increasing the intensity of the stressor has a greater positive effect on the abundance of the stressor-resistant species via its release from competitive inhibition than it has a negative effect via mortality (or decreased fecundity) of the stressor-resistant species. For instance, the equilibrium abundance of species i, denoted N_i^*, is given by Eq. (7a) if it has no competitor, and N_i^* is given by Eq. (7b) if there is a second competitor, j ($j \neq i$)

$$N_i^* = \frac{r_i}{a_{ii}}(1-v_iE) \tag{7a}$$

$$N_i^* = \frac{1}{1-o_{ij}^2}\left[\frac{r_i}{a_{ii}}-\frac{a_{ij}\,r_j}{a_{ii}\,a_{jj}} + E\left(\frac{a_{ij}\,r_j}{a_{ii}\,a_{jj}}v_j-\frac{r_i}{a_{ii}}v_i\right)\right]. \tag{7b}$$

A hydra effect for species i (i.e., $\frac{\partial N_i^*}{\partial E} > 0$) requires that $\frac{a_{ij}r_j}{a_{ii}a_{jj}}v_j > \frac{r_i}{a_{ii}}v_i$. This inequality has a straightforward interpretation: species i experiences a hydra effect if the direct effect of stressor mortality (or decreased fecundity) on its equilibrium abundance ($\frac{r_i}{a_{ii}}v_i$, because $\frac{\partial N_i^*}{\partial E} = -\frac{r_i}{a_{ii}}v_i$, with no competition) is

smaller than the indirect benefit—via competition—of stressor mortality on its competitor's abundance ($\frac{a_{ij}r_j}{a_{ii}a_{jj}}v_j$, which captures the direct effect of stress on species j's equilibrium abundance, $\frac{r_j}{a_{jj}}v_j$, multiplied by the strength of competition exerted by species j relative to species i's density dependence, $\frac{a_{ij}}{a_{ii}}$) (Fig. 1e).

Ecosystem thinning and niche-correlated stressors

In the previous section, we showed that relatively little stress is needed to disrupt the coexistence of pairs of species with high ecological similarity (measured by o_{ij}) and differing sensitivity to the stress (measured by v_i). As a result of this—unless there was perfect correlation between sensitivity and niche, such that highly ecologically similar species did not differ in sensitivity to stress—we would expect to see broadly inflicted stressors cause competitive exclusions, at low intensity, within groups of ecologically similar species. We call this ecosystem thinning. We would expect to see ecosystem thinning be most pronounced with stress that is inflicted broadly across niche space, but with little correlation between sensitivity and niche.

Consider the equilibrium abundance of species i in the I-species coexistence equilibrium, N_i^*, which can be derived from Eq. (1)

$$N_i^* = \sum_{j=1}^I a_{-ij}r_j(1-v_jE).$$ (8)

Here, a_{-ij} is the ith-row and jth-column element of $\mathbf{A}^{-1}$, the inverse of the matrix of density dependence and competition coefficients, $\mathbf{A}$ (a_{ij} as the ith-row and jth-column element of $\mathbf{A}$). Recall also that $a_{-ij} = \frac{C_{ji}}{\det\mathbf{A}}$, where C_{ji} (the cofactor) is the signed determinant of the sub-matrix of $\mathbf{A}$ obtained by removing its jth row (measuring competitive impacts of all species on species j) and ith column (measuring species i's competitive impacts on other species). The proportional effect of a small change in the stressor intensity on N_i^* is

$$\frac{\partial N_i^*}{N_i^*\partial E} = \frac{-\sum_{j=1}^I a_{-ij}r_jv_j}{\sum_{j=1}^I a_{-ij}r_j(1-v_jE)} = \frac{-\sum_{j=1}^I C_{ji}r_jv_j}{\sum_{j=1}^I C_{ji}r_j(1-v_jE)}.$$ (9)

If all species have the same sensitivity, v (i.e., $v_i = v$ for all i), Eq. (9) reduces to

$$\frac{\partial N_i^*}{N_i^*\partial E} = \frac{-v}{1-vE}.$$ (10)

In other words, if all species have the same sensitivity, increasing the stressor intensity decreases all species' equilibrium abundances proportionally but does not affect the species composition (until the level at which all species are driven extinct) or

their relative abundances. If, however, species differ in their sensitivities, species with the largest values of $\sum_{j=1}^S C_{ji}r_jv_j$ will decline proportionally fastest as the stressor intensity increases, and vice versa. Cofactors do not easily lend themselves to intuitive biological interpretation, but it logically follows from our analysis in two-species models above that species with high sensitivity to stress relative to ecologically similar species will decline in abundance the fastest (e.g., see Fig. 2).

In Fig. 2, we illustrate the ecosystem thinning concept in a simulation, using an explicit, cardinal niche axis. Following MacArthur and Levins (1967), we assume that the resource is rapidly replenishing, and each species has a bell-shaped resource utilization curve along the niche axis, where we denote the resource utilization of species i at niche position y: $R_i(y)$. We assume that $R_i(y)$ has the shape of a normal distribution's PDF, with mean y_i and standard deviation w_i: $R_i(y) = K_i\mathrm{PDF}[N(y_i, w_i)]$, where K_i is the carrying capacity of species i (Fig. 1a). Thus, the area under the resource utilization curve for species i is K_i (similarly to Fig. 1 in MacArthur and Levins 1967). Following MacArthur and Levins (1967), we calculate the competition coefficients as

$$a_{ij} = \left(\frac{r_i}{K_i}\right)\frac{\int R_i(y)R_j(y)dy}{\int [R_i(y)]^2 dy}.$$ (11)

We assemble the community under no stress ($E = 0$) from a species pool of 100 species, with randomly chosen parameter values (see Fig. 2 caption for parameter distributions), and we approximate equilibrium by simulating 100 time steps. Of the species that coexist without stress (defined in our simulation as those with abundances greater than 10^{-7} at $t = 100$), we simulate their equilibrium abundances ($t = 100$) under varying intensities of the stressor, in each of three scenarios regarding sensitivity: (a) (black) all species have identical sensitivity ($v_i = 0.2$ for all i) (Fig. 2a); (b) (red) each species has a sensitivity randomly drawn from uniform distribution, $U[0.15, 0.25]$ (Fig. 2b); and (c) (blue) species have sensitivities determined by their niche position (y_i), such that sensitivity is greatest for a particular niche (y^T), which we can think of as *targeted* by the stressor (e.g., a particular prey type in a bait fishery), and sensitivity decreases the further away from y^T a species' niche is: $v_i = 0.15 + 0.5\mathrm{PDF}[N(y^T, 2)]$, where $y^T = 5$ (Fig. 2c). The mean sensitivity ($\bar{v} = 0.2$) is the same in all three scenarios.

Scenario (a) is meant as a control: with all species having the same sensitivities, the stressor does not affect coexistence and instead reduces the equilibrium abundance of each species proportionally as it increases in intensity (Fig. 2d). In scenario (b), we see ecosystem thinning: a small number of species, relatively evenly spaced along the niche axis and relatively insensitive to the stressor compared to their niche neighbors, emerge as dominant, some initially increasing in abundance (hydra effects) (Fig. 2e). In scenario (c), sensitivity to the stressor is not uniform, but it is highly correlated
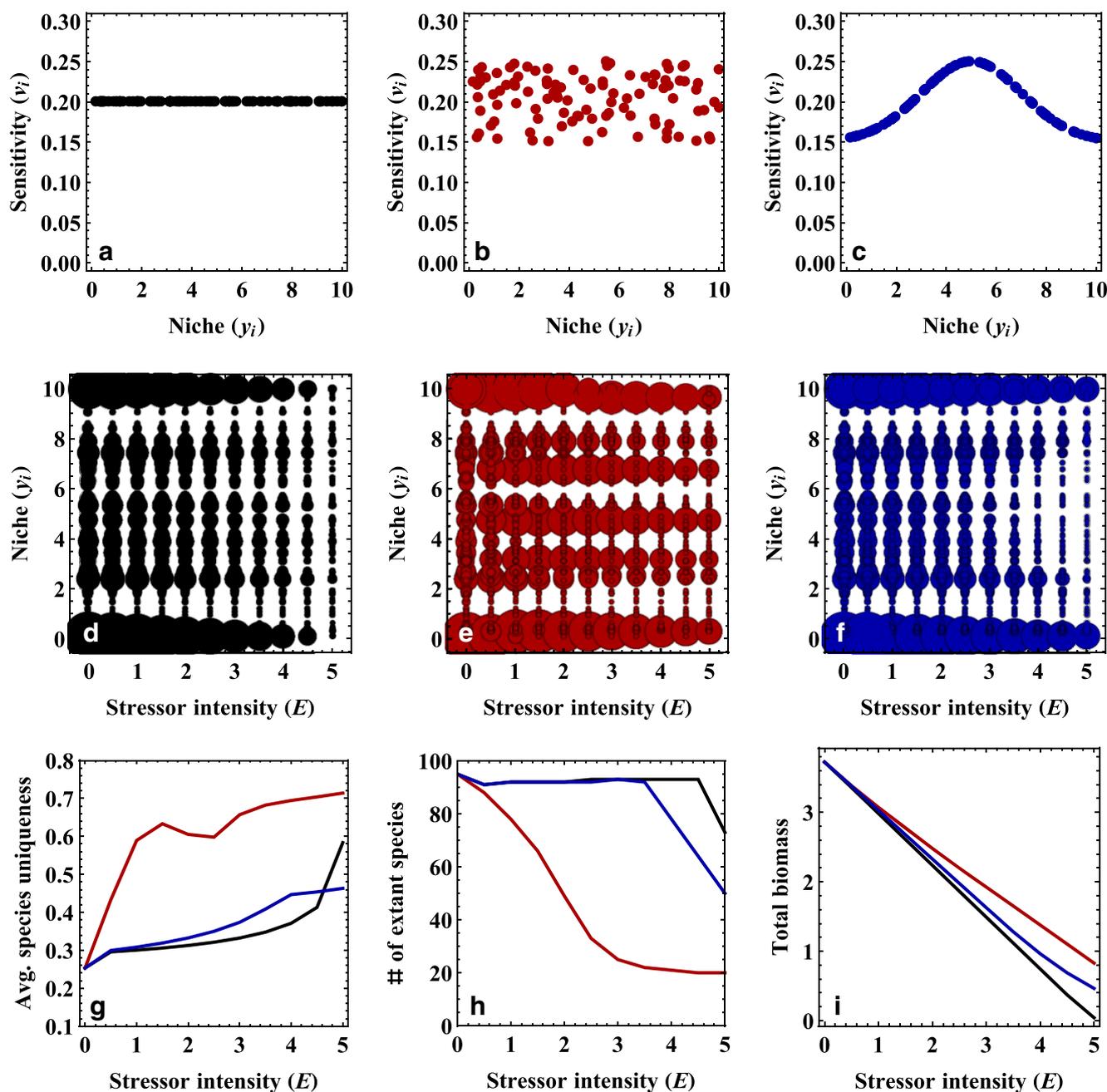
Fig. 2 Ecosystem thinning. We assemble communities of 100 species, each with randomly drawn parameter values ($r_i \sim U[0.5, 2.5]$; $y_i \sim U[0, 10]$; $w_i = K_i = 1$). For the sub-set of these species that coexists without stress ($E = 0$), we then simulate equilibria (approximated by the state at $t = 100$), in each of three sensitivity scenarios [(a), (b), and (c) in the main text]. The mean sensitivity among all species ($\bar{v} = 0.2$) does not differ across the three scenarios, but the pattern of species-specific sensitivity relative to niche (y_i for species i) does differ. Namely, in scenario (a) (black), all species have the same sensitivity ($v_i = 0.2$ for all i) (**a**); in scenario (b) (red), sensitivities are randomly drawn for each species from $U[0.15, 0.25]$ and uncorrelated with niche (**b**); and in scenario (c) (blue), sensitivities are determined by niche position (y_i) (see text for details) (**c**). **d–f** The equilibrium abundances (represented by the bubble sizes) of each species at different stressor intensities in each scenario (color-coded), with species niche also shown. **g–i** The average species uniqueness (see text for definition), the number of extant species (i.e., having abundance greater than 10^{-7}), and the total biomass, respectively, in each scenario (color-coded) at varying stressor intensities

with niche position, meaning that niche neighbors have similar sensitivities. Here, there are fewer extinctions at low stressor intensity than in scenario (b), but abundance reductions and extinctions are concentrated among species with niches close to y^T ($y^T = 5$) (Fig. 2f).

To illustrate ecosystem thinning graphically in our simulation (Fig. 2g), it is useful to define a measure of species uniqueness (i.e., how ecologically dissimilar species are from one another). Under ecosystem thinning, we would expect the average species uniqueness to increase.

In our simulation, we define the uniqueness of species i, denoted U_i, as

$$U_i = \frac{N_i}{\sum_{j=1}^{I} N_j o_{ij}}. \tag{12}$$

Recalling that $o_{ii} = 1$ (and thus, $o_{ii} N_i = N_i$), $U_i = 1$ if species i is totally unique (i.e., if $o_{ij} = 0$ for all $j \neq i$). U_i is relatively large if species ecologically similar to species i have relatively lower abundances (i.e., if N_j is small, relative to N_i, when o_{ij} is large), and U_i is small in the opposite case (i.e., if N_j is large, relative to N_i, when o_{ij} is large). Under ecosystem thinning, we would expect to see a relatively small number of species—relatively insensitive to stress and spread out across niche space—emerge as dominant under stress. Thus, we should see average species uniqueness increase under ecosystem thinning. For our simulation, we measure average species uniqueness, denoted $\overline{U}$, as an abundance-weighted average of U_i across species

$$\overline{U} = \frac{\sum_{i=1}^{I} U_i N_i}{\sum_{i=1}^{I} N_i}. \tag{13}$$

Notice that, in contrast to ecosystem thinning, if all species have the same sensitivity (i.e., $v_i = v$ for all i), we would expect $\overline{U}$ at equilibrium to be the same under any stressor intensity, because equal sensitivities make relative abundances at equilibrium unaffected by stress [see Eq. (10)].

Figure 2g–i shows changes in average species uniqueness weighted by abundance ($\overline{U}$), the number of extant species, and the total biomass ($\sum_{i=1}^{I} N_i$), respectively, in each of the three sensitivity scenarios, at equilibrium ($t = 100$), as the stressor intensity increases. In scenario (b) (red, ecosystem thinning), the number of extant species decreases much more rapidly, as the intensity of the stressor increases, than in the other scenarios because of extinctions within groups of ecologically similar competitors (Fig. 2h). In contrast, increasing the stressor intensity causes the total biomass to decrease more slowly in scenario (b) than in the other scenarios, because ecosystem thinning selects for relatively insensitive species while still preserving much of the functional diversity (Fig. 2i). Similarly, the average species uniqueness increases in scenario (b), both in absolute terms and relative to the other two scenarios (Fig. 2g). Indeed, in scenario (a) (all species have the same sensitivity), equilibrium uniqueness is analytically constant, because relative abundances are invariant to E in this scenario (note that uniqueness only appears to have a slight upward trend in the simulation due to the approximation of equilibrium by $t = 100$, which becomes less accurate in measuring relative equilibrium abundances when E is large and these abundances are small).

Discussion

Main theoretical insights

That more ecologically similar species interact more strongly is a fundamental principle in ecology. This principle plays an important role in shaping coexistence and community assembly. Its logic underpins several decades of theory (see, e.g., Abrams 1983; Chesson 2000; Meszéna et al. 2006; Letten et al. 2017) that has shown that ecologically similar species need to also be similar in competitive ability to coexist with each other (or face universal competitive tradeoffs; see Tilman 2011). Here, we have examined how broadly inflicted stressors—stressors that inflict mortality or decreased fecundity on many species simultaneously—can have indirect effects on community composition by interacting with these competitive forces. Humans broadly inflict a large number of intense stressors, including habitat destruction, pollution, climate change, multispecies harvesting, invasive species, and others, which constitute many of humanity's greatest threats to the biosphere (Maxwell et al. 2016). We find that such stressors likely exacerbate disparities in competitive ability—and consequently cause disproportionate competitive exclusions within groups of ecologically similar species—as the stressors increase in intensity, except in the unlikely special case where species' competitive abilities are identically impacted by the stressors, per unit intensity. We demonstrate this result in a simple model of Lotka-Volterra-style competition in the main text (Fig. 1) and show that it is robust to three qualitatively different models of mechanistic competition in the Appendix (Fig. 3).

From this simple insight, we demonstrate several theoretical corollaries with important implications for community ecology in the Anthropocene. First, increasing the intensity of broadly inflicted stressors can cause what we refer to as "ecosystem thinning," whereby those species that survive are spread out in niche space and may become more abundant, while richness and redundancy decrease, unless the stressor is highly niche-correlated or targeted (Fig. 2). By reducing redundancy, ecosystem thinning may reduce the temporal stability of ecosystem functions (Lehman and Tilman 2000; Loreau and de Mazancourt 2013). However, ecosystem thinning also buffers ecosystem productivity by selecting (in an ecological sense analogous to the evolutionary sense; see Price 1970 and Loreau and Hector 2001) for low-sensitivity species. Thus, ecosystem thinning results in a smaller loss of productivity than would the proportional decrease in abundance of all species (Fig. 2i). For similar reasons, ecosystem thinning likely also results in a smaller loss of productivity than would the exclusion of the same number of randomly chosen species.

Second, our theory predicts that the stressor intensity needed to indirectly exclude a species by upsetting competitive
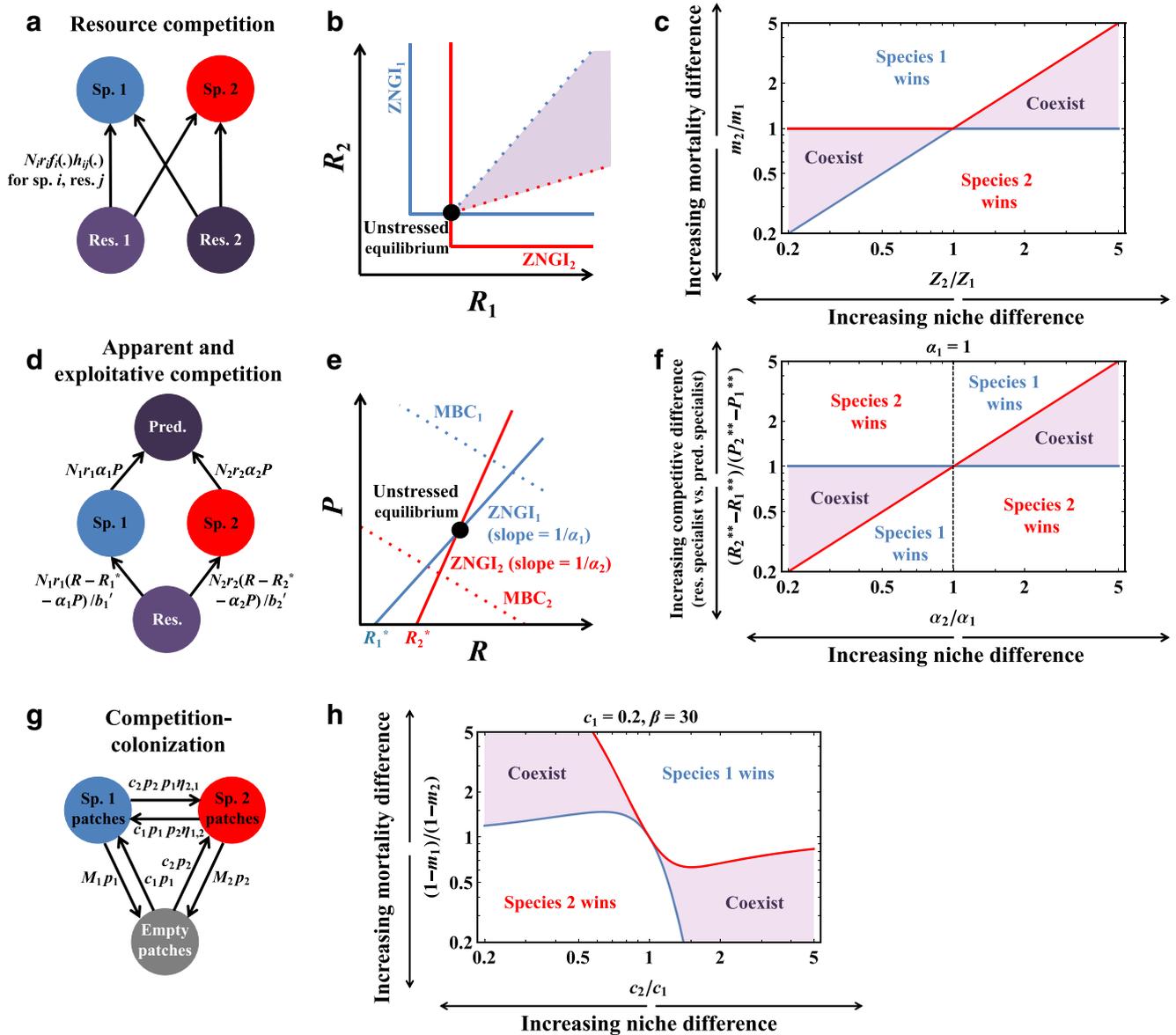
Fig. 3 Weak limiting similarity in three mechanistic models of two-species competition. **a**, **d**, **g** The structure of the three models. **b**, **e** Zero-net-growth isoclines [resource concentrations (**b**) and mass-balance constraints (**e**)], allowing coexistence in models 1 and 2, respectively. **c**, **f**, **h** How the range of parameter values permitting coexistence, in each model, shrinks as the species become more similar in ecological niche. This is weak limiting similarity

coexistence will often be much smaller than the stressor intensity needed to directly cause species extinction by making mortality larger than the maximum growth rate (Fig. 1d). The species excluded indirectly in this manner are those with high sensitivity to the stressor relative to their competitors.

Third, in multispecies competitive communities, species with low sensitivity to stressors relative to their ecologically similar competitors can increase in abundance as the intensity of the stressor increases via *hydra effects* (Fig. 1e). This occurs when the indirect benefit of the stressor killing these species' more sensitive competitors more than offsets the direct negative effect of mortality caused by the stressor. Aalto and

Baskett (2013) also theoretically demonstrate this effect in the context of multispecies fisheries, and several studies (e.g., Hastings 1980; see also Nee and May 1992; Tilman et al. 1994; Huxel and Hastings 1998) demonstrate similar phenomena in the context of disturbance or habitat destruction in competition-colonization models.

Assumptions and limitations

We demonstrate our main results to be robust to several different types of competition models, but our analysis also has some noteworthy restrictions in scope. First, we focus on

Table 1 Model parameters

Model/parameter	Definition
Main text model	
N_i	Abundance of species i
r_i	Maximum per-capita growth rate of species i
a_{ij}	Per-capita inhibitory effect of species j on the per-capita growth rate of species i
v_i	Sensitivity of species i to the stressor (per-capita, per-unit-intensity mortality rate divided by r_i)
E	Intensity of the stressor
o_{ij}	Ecological similarity between species i and species j
E_c	Intensity of the stressor that causes competitive exclusion of the more sensitive of 2 competitors
$E_{c,i}$	The stressor intensity needed to cause extinction of species i with no competition
$\mathbf{A}$	The species-interaction matrix, whose ith-row, jth-column element is a_{ij}
C_{ji}	The j, ith cofactor of $\mathbf{A}$: the signed determinant of the sub-matrix of $\mathbf{A}$ obtained by removing its jth row (measuring competitive impacts of all species on species j) and ith column (measuring competitive impacts of species i on all species)
$R_i(y)$	The resource utilization of species i at niche position y
y_i	Mean of species i's resource-utilization curve (i.e., a measure of species i's niche position)
w_i	Standard deviation of species i's resource-utilization curve (i.e., a measure of species i's niche width)
K_i	Carrying capacity of species i, and the area under species i's resource-utilization curve
U_i	Measure of species i's uniqueness
$\overline{U}$	Abundance-weighted average uniqueness across all species in the community
Appendix model 1: resource competition	
N_i	Abundance of species i
R_j	Abundance of resource j
m_i	The natural mortality rate of species i
r_i	Scale of turnover of species i
v_i	Sensitivity of species i to the stressor (per-capita, per-unit-intensity mortality rate divided by $r_i m_i$)
E	Intensity of the stressor
$g_j(R_j)$	The growth rate of resource j in the absence of consumption by the 2 competing species
$f_i(R_1, R_2)$	The growth rate of species i as a function of resources, as a fraction of the turnover rate, r_i
$h_{ij}(R_1, R_2)$	The conversion rate of resource j into species i
Z_i	The resource ratio required by species i—a univariate measure of its niche
$R_{ji}{}^*$	The minimum concentration of resource j allowing the persistence of species i
E_c	Intensity of the stressor that causes competitive exclusion of the more sensitive of 2 competitors
Appendix model 2: apparent and exploitative competition	
P	Abundance of the predator
N_i	Abundance of competitor i
R	Abundance of the resource
a_i	Consumption rate of competitor i by predators
b_i	Conversion rate of competitor i consumed into predator biomass
d	Natural death rate of predators
a_i'	Consumption rate of resource by competitor i
b_i'	Conversion rate of resource consumed into competitor i biomass
d_i'	Natural death rate of competitor i
r_i	Scale of turnover of species i
α_i	The amount of additional resources species i needs, per additional predator—the key measure of species i's niche
s	Total resource supply (the system is assumed to be closed); can be a function of stress $[s(E)]$
b_P	Effective conversion rate of resources into predators
$R_i{}^*$	Minimum resource abundance on which species i can survive if there are no predators or stressors
$R_i{}^{**}$	Equilibrium resource abundance that would occur with no stressor and only competitor i
$P_i{}^{**}$	Equilibrium predator abundance that would occur with no stressor and only competitor i

Table 1 (continued)

Model/parameter	Definition
γ_i	Per-capita, per-unit-intensity mortality rate of species i from the stressor, divided by r_i
E	Intensity of the stressor
R_i'	Equilibrium resource abundance that would occur with stressor intensity E and only competitor i (with the other competitor not present)
P_i'	Equilibrium predator abundance that would occur with stressor intensity E and only competitor i (with the other competitor not present)
E_c	Intensity of the stressor that causes competitive exclusion of the more sensitive of 2 competitors
Appendix model 3: competition-colonization tradeoff	
p_i	Proportion of sites occupied by species i
c_i	Colonization rate of unoccupied sites by species i
M_i	Extinction rate of species i from occupied sites
m_i	Standardized mortality measure, measuring mortality as a fraction of the colonization rate ($m_i = M_i/c_i$)
$\eta_{i,j}$	Success rate of species i at displacing species j
ω_i	Parameter determining the tradeoff between colonization and competition for species i [$\omega_i = \exp(-\beta c_i)$]
β	Parameter determining the tradeoff between colonization and competition for both species
γ_i	Per-unit-intensity extinction rate of species i from occupied sites, caused by the stressor, divided by $c_i p_i$
m_{i0}	Baseline natural mortality (extinction rate from occupied patches) for species i
E	Intensity of the stressor
E_c	Intensity of the stressor that causes competitive exclusion of the more sensitive of 2 competitors

equilibrium statics and do not consider the effects of stressors whose intensities are coupled to the species' abundances, nor do we consider effects on the stability of equilibria, species abundances, or other community properties. Some stressors' intensities (e.g., climate change, many forms of pollution) are likely not tightly coupled to species' abundances, but other stressors (e.g., fisheries and other harvests) are coupled to the abundances of the species they impact (e.g., Clark 1976). Anthropogenic stressors have been shown to have important effects on the stability of some species' abundances. For instance, Anderson et al. (2008) showed that fisheries can amplify fluctuations in larval fish abundances by truncating population age structure.

Second, we focus on theoretical communities that would coexist in the absence of the stressor, and thus, we do not consider the possibility of stressors facilitating new invasions. Species with low competitive ability, but also low sensitivity to the stressor, compared to established species, could be facilitated in this manner. Indeed, the potential for disturbance or generalist predators—both conceptually equivalent to our broadly inflicted stressor—to facilitate coexistence has already been shown in a number of previous studies (e.g., Grover 1997; Hastings 1997; Chesson 2000). The relative prevalence of facilitated invasions to competitive exclusions would likely depend on the spatial scale of the community being focused on, the diversity and connectivity of the larger meta-community, and, of course, how likely such potential invaders are to exist in the first place given the absence of the conditions enabling their invasion throughout geologic time.

Third, we focus on deterministic models and do not consider interactions between stressors and the stochastic forces contributing to community structure. These forces have been shown (Chisholm and Pacala 2010) to be most important relative to competitive forces when examining sub-communities within highly diverse and well-connected meta-communities. Thus, our results should be interpreted cautiously in ecological contexts having these properties.

Testable predictions

Our main result and its corollaries provide some empirically testable predictions. For instance, field studies, similar to Stubbs and Wilson's (2004) study of functional traits in sand dune plant communities to test for limiting similarity, could be repeated along gradients of anthropogenic or environmental stress. Finding greater dissimilarity in more stressed environments would lend support to our theory. Similarly, our theory predicts hydra effects in species with more stressor-sensitive ecologically similar competitors. Finding a species increasing in abundance as intensity of stressors (e.g., fishing pressure) increases, affecting both the focal species and its competitors, would lend suggestive support to our theory. However, empirically demonstrating that apparent hydra effects are mediated specifically by competition, and not either by some other mechanisms or by a coincidental effect (and thus not a hydra effect), could be challenging. This empirical challenge is compounded by the fact that estimates of mortality rates caused by stressors, growth rates, and other important factors

are all susceptible to being biased by the fact that species interactions are typically difficult to directly observe or quantify (e.g., see Burgess et al. 2017 for an analysis of this issue in a fisheries context). Similarly, it may be difficult to empirically test our prediction that indirect competitive exclusions occur at lower stressor intensities than direct extinctions from mortality, because empirical measures of direct mortality from stressors may inadvertently include indirect effects on mortality. Nonetheless, there is already empirical evidence for anthropogenic stressors—such as fertilization (e.g., Harpole and Tilman 2007; Socher et al. 2012), climate change (e.g., Walther et al. 2002; Cahill et al. 2012; Ockendon et al. 2014), and fishing (e.g., Jackson et al. 2001; Szuwalski et al. 2017)—substantially affecting community structures via indirect, ecologically mediated mechanisms, as much as or more than by direct mortality. Microcosm or mesocosm experiments could overcome some of these empirical challenges listed above and have been a powerful and popular tool for testing ecological theories (e.g., Titman 1976; Hastings and Costantino 1987; Melbourne and Hastings 2009).

Management implications

Our results have several important implications for conservation and management. First, they suggest that indirect effects of anthropogenic stressors on species, mediated by ecological interactions, could be as much as or more important than direct effects. As mentioned above, there is already empirical evidence for this in some cases. For instance, nutrient loading can disrupt competitive coexistence by effectively removing a niche dimension, which prevents niche tradeoffs from facilitating coexistence (e.g., Harpole and Tilman 2007). Climate change and invasions can change patterns of species co-occurrence, which disrupts predator-prey interactions (e.g., Urban et al. 2016; Pecl et al. 2017). Overharvesting can initiate trophic cascades (e.g., Jackson et al. 2001).

Second, if broadly inflicted anthropogenic stressors primarily reduce diversity *within* functional groups (i.e., ecosystem thinning), they may reduce the temporal stability of important ecosystem functions more rapidly than they reduce flows of ecosystem services. Flows of some ecosystem services, such as productivity, are primarily bolstered by diversity *across* functional groups creating complementarity (see Hooper et al. 2005 for review). By maintaining functional diversity and selecting for relatively stress-resistant species within each functional group, ecosystem thinning may buffer such flows of ecosystem services to stress. Indeed, this process provides one possible explanation for the saturating relationship between biodiversity and ecosystem function often observed (see Schwartz et al. 2000 for review). Putting these predictions together, the near-term ability of some ecosystems to provide services, despite high levels of anthropogenic stress, may belie

already incurred losses of redundancy from ecosystem thinning, which could imply decreased resilience to additional stress.

Third, our prediction that broadly inflicted stressors can cause fewer competitive exclusions if they are niche-correlated (Fig. 2), may have implications for management of stressors in which niche targeting is possible. For instance, this result may imply lower competitive impacts from niche-targeting fishing methods, such as baited hooks, relative to more niche-generalist methods, such as trawls. However, much more work needs to be done to test and contextualize this prediction, beyond our simple model shown in Fig. 2, before it should be applied directly to management in fisheries or other systems.

Conclusion

We theoretically examine how competitive exclusion interacts with broadly inflicted stressors that cause mortality or decreased fecundity for many species simultaneously. Broadly inflicted stressors found in nature include many of the greatest human threats to biodiversity. For communities of previously coexisting species, our theory predicts that increasing stressor intensities should generally result in *thinner* communities, consisting of fewer and more ecologically dissimilar species. Although more work is needed to refine this conclusion in stochastic and transient contexts, it follows logically from well-established and general theoretical principles: (i) that more ecologically similar species need to be more similar in competitive ability to coexist (Abrams 1983) and (ii) that coexistence among progressively similar species is progressively more fragile to perturbation (Meszéna et al. 2006). Our results highlight the importance of indirect, ecologically mediated, effects of anthropogenic stressors, which merit a much greater study than they have yet received.

Appendix. Weak limiting similarity and broadly inflicted stress in mechanistic models

Our main results follow from the weak limiting similarity principle: the more ecologically similar two species are, the

more competitively similar they must be to coexist and the smaller the perturbation needed to upset coexistence. In the context of broadly inflicted stress, weak limiting similarity implies that—barring the special case where the stressor identically impacts species' competitive abilities—lower-intensity stress is needed, on average, to upset the coexistence between more ecologically similar species. We demonstrate this principle in a Lotka-Volterra-type competition model in the main text. Below, we show that principle is robust to each of three qualitatively different mechanistic competition models (Fig. 3) (see Table 1 for all parameter definitions).

Model 1: resource competition

Our first model is based on Tilman's (1980) model of two species competing for two limiting resources (Fig. 3a). The abundances of these resources (1 and 2) are denoted R_1 and R_2. We assume that the rates of change in abundance of species i and resource j are given by

$$\frac{dN_i}{N_i dt} = r_i[f_i(R_1, R_2) - m_i(1 + v_i E)] \tag{14}$$

$$\frac{dR_j}{dt} = g_j(R_j) - \sum_{i=1}^{2} N_i r_i f_i(R_1, R_2) h_{ij}(R_1, R_2). \tag{15}$$

Here, $g_j(.)$ is a function describing the growth rate of resource j in the absence of consumption by the species, $f_i(.)$ describes the growth rate of species i as a function of resources, m_i is the natural mortality rate of species i, and $h_{ij}(.)$ describes the conversion rate of resource j into species i. To be consistent with the other models in our analysis, we add the parameter r_i (which Tilman 1980 does not use) to represent the scale of turnover of species i. Thus, f_i and m_i in our model are normalized measures. We also normalize sensitivity (v_i) by m_i. This allows v_i (sensitivity) to have a similar interpretation as it does in the main text. The parameter r_i does not quite represent the maximum per-capita growth rate here—as it does in the main text—but serves an analogous function, by measuring the scale of turnover, as we will see below.

For simplicity, we focus our analysis on the case of essential resources—in which the resource ratio required by each species provides a univariate measure of its niche, which we denote Z_i for species i. However, we conjecture that our main result should also hold with most other types of resources analyzed in Tilman 1980. We define r_i such that f_i can be expressed as

$$f_i(R_1, R_2) = \min\{R_1, Z_i R_2\}. \tag{16}$$

The fact that the resources are essential is captured by the fact that species i grows according to the smaller value of R_1 and $Z_i R_2$; thus, Z_i represents the amount of resource 1 relative to resource 2 that species i needs to grow (the resource ratio), which is the key measure of the niche in this model. For

instance, a species' niche in this type of model might be how much light or phosphorus it needs relative to water or nitrogen (e.g., Titman 1976).

With these assumptions, the minimum concentrations of the resources allowing the persistence of species i (i.e., allowing $\frac{dN_i}{dt} \geq 0$), denoted R_{1i}^* and R_{2i}^* for species i, are

$$R_{1i}^* = m_i(1 + v_i E) \tag{17}$$

$$R_{2i}^* = \frac{m_i}{Z_i}(1 + v_i E). \tag{18}$$

Tilman (1980) showed that a necessary condition for the coexistence of the two species in this model is that if $R_{1i}^* < R_{1j}^*$, $R_{2i}^* > R_{2j}^*$. In other words, the two species can only coexist if whichever is the superior competitor with respect to resource 1 (i.e., with a lower R_{1i}^*) is the inferior competitor with respect to resource 2 (higher R_{2i}^*) (Fig. 3b). If one species was a better competitor with respect to both resources, it would outcompete the other. With no stressor ($E = 0$), this necessary condition for coexistence (i.e., if $R_{1i}^* < R_{1j}^*$ then $R_{2i}^* > R_{2j}^*$) amounts to

$$1 < \frac{m_j}{m_i} < \frac{Z_j}{Z_i}, \text{when } m_j > m_i., \tag{19}$$

With the addition of the stressor ($E > 0$), the analogous necessary condition for coexistence is

$$1 < \frac{m_j(1 + v_j E)}{m_i(1 + v_i E)} < \frac{Z_j}{Z_i}, \text{when } m_j > m_i. \tag{20}$$

Equations (19) and (20) are analogous to Eqs. (3a) and (3b), from the main text (Fig. 3c). The more ecologically similar the two species (i.e., the closer Z_i/Z_j is to 1), the smaller the range of relative mortality rates (m_j/m_i) allowing coexistence. If $v_i = v_j$, increasing the stressor intensity does not perturb coexistence, but if $v_i > v_j$, species i will become less competitive (i.e., $\frac{m_j(1 + v_j E)}{m_i(1 + v_i E)}$ will decrease) as E increases. The limit of $\frac{1 + v_j E}{1 + v_i E}$, as E approaches infinity, is $\frac{v_j}{v_i}$, so even with $v_i > v_j$, necessary coexistence Eq. (20) cannot be disrupted by stress if the difference in sensitivity is too small relative to the difference in mortality rate: specifically, if $\frac{v_i}{v_j} < \frac{m_j}{m_i}$ when $m_j > m_i$, or equivalently, if $\frac{v_i}{v_j} < \frac{m_i}{m_j}$ when $m_i > m_j$. However, m_i/m_j approaches 1 as Z_i/Z_j approaches 1, among pairs of coexisting species [by Eq. (20)], making the minimum sensitivity difference permitting competitive exclusion [by Eq. (20)] vanish as the niches approach total similarity (i.e., as Z_i/Z_j approaches 1). If sensitivity differences are sufficiently large to allow competitive exclusion by increasing stress (E) according to Eq. (20), the stressor intensity causing competitive exclusion of species i, when $v_i > v_j$, is bounded by

$$0 < E_c \leq \dfrac{\dfrac{Z_j}{Z_i}-1}{v_j\left(\dfrac{v_i}{v_j}-\dfrac{Z_j}{Z_i}\right)}, \text{ when } m_j > m_i \text{ (implying } Z_j > Z_i) \qquad (21a)$$

$$0 < E_c \leq \dfrac{\dfrac{Z_i}{Z_j}-1}{v_j\left(\dfrac{v_i}{v_j}-\dfrac{Z_i}{Z_j}\right)}, \text{ when } m_i > m_j \text{ (implying } Z_i > Z_j). \qquad (21b)$$

This is analogous to Eq. (4) in the main text and has an analogous interpretation—the upper bound approaches zero as the niches approach total similarity (i.e., as Z_i/Z_j approaches 1).

Model 2: apparent and exploitative competition

Our second model is based on Holt et al.'s (1994) model of apparent and exploitative competition (Fig. 3d). Here, the two competing species compete directly for a single resource, with abundance R. They also indirectly compete via sharing a predator, having abundance P. In the absence of stressors ($E = 0$), the system is assumed to be closed, such that there is a constant supply (s) of total resource in the system, which transfers between forms (resource, competitor, predator). The dynamics of the system, without the stressor, are given by

$$\frac{dP}{Pdt} = \sum_{i=1}^{2} a_i b_i N_i - d \qquad (22)$$

$$\frac{dN_i}{N_i dt} = r_i[R - R_i^* - \alpha_i P], \text{ where } r_i = a_i' b_i', R_i^* = \frac{d_i'}{r_i} \text{ and } \alpha_i = \frac{a_i}{r_i} \qquad (23)$$

$$R = s - \sum_{i=1}^{2} \frac{N_i}{b_i'} - \frac{P}{b_P}. \qquad (24)$$

Here, a_i is the consumption rate of competitor i by predators; b_i is the conversion rate of competitor i consumed into predator biomass; $a_i' b_i'$ is the analogous consumption and conversion rates, from resources into competitor i; d and d_i' are the natural death rates, of predators and competitor i, respectively; and b_P is the effective conversion rate of resources into predators. The other variables defined in Eq. (23) are useful permutations of these. For instance, R_i^* is the minimum resource abundance on which species i can survive if there are no predators or stressors (Holt et al. 1994).

Following Holt et al. (1994), we denote the equilibrium resource and predator abundances that would occur with no stressor and only competitor i, R_i^{**}, and P_i^{**}, respectively. These, together with R_i^*, determine species i's niche, and they can be derived from Eqs. (22) to (24)

$$R_i^{**} = R_i^* + \alpha_i P_i^{**}. \qquad (25)$$

$$P_i^{**} = \frac{b_P\left(s a_i b_i b_i' - d - R_i^* a_i b_i b_i'\right)}{a_i b_i b_i'(\alpha_i b_P + 1)}. \qquad (26)$$

Stable coexistence requires both species to be able to increase when rare. For species i, this means that $\frac{dN_i}{dt} > 0$ [from Eq. (23)] when $N_i \approx 0$, $R = R_j^{**}$, and $P = P_j^{**}$. Without the stressor, this condition is equivalent to

$$R_j^{**} - R_i^{**} > \alpha_i\left(P_j^{**} - P_i^{**}\right). \qquad (27)$$

Re-arranging Eq. (25), we see that

$$\alpha_i = \frac{R_i^{**} - R_i^*}{P_i^{**}}. \qquad (28)$$

Thus, the parameter α_i is the key measure of the niche for our purposes. It measures the amount of additional resources species i needs, per additional predator. Coexistence without the stressor requires an implicit tradeoff between resource use and predator resistance (Holt et al. 1994) (Fig. 3e). We can see this from inequality Eq. (27), which cannot hold for both species (each having positive α) unless $(R_j^{**} - R_i^{**})$ and $(P_j^{**} - P_i^{**})$ have the same sign—meaning that whichever species can survive on fewer resources (lower R^{**}) must also be able to tolerate a lower predator abundance (lower P^{**}). The parameter α_i effectively measures where, on this tradeoff, species i lies: small α_i means that species i needs relatively few additional resources to cope with additional predators (i.e., it specializes in predator resistance), and large α_i means species i's resource requirements increase significantly as predators become more abundant, meaning it would have to be a better resource competitor to coexist.

Suppose species j is the inferior resource competitor, but is less susceptible to predation, such that $R_j^{**} > R_i^{**}$ and $P_j^{**} > P_i^{**}$. In this case, we can simultaneously express the coexistence criterion Eq. (27) for both species as

$$\alpha_i < \frac{R_j^{**} - R_i^{**}}{P_j^{**} - P_i^{**}} < \alpha_j, \text{ when } R_j^{**} > R_i^{**} \text{ and } P_j^{**} > P_i^{**}. \qquad (29)$$

Coexistence Eq. (29) is analogous to coexistence Eqs. (19) and (3a) from the previous models (Fig. 3f). The more similar the two species' niches (measured by α_i and α_j) are, the more similar their competitive abilities must be to coexist. As α_i approaches α_j, coexistence requires $\frac{R_j^{**} - R_i^{**}}{P_j^{**} - P_i^{**}}$ approach 1, and any small perturbation in R_i^{**}, R_j^{**}, P_i^{**}, or P_j^{**}, caused by a stressor, would disrupt coexistence.

Suppose that stress (having intensity E) negatively affects the per-capita growth rate of the two consumer species (1 and 2) in some way. By increasing mortality on the consumer species, stress would have a positive direct effect on R_i^{**} (because species i needs more resources to offset higher mortality), but it will have a negative indirect effect on both R_i^{**} and

P_i^{**} by reducing the efficiency with which resources are passed through the food chain to predators (which lowers R_i^{**} by reducing predation pressure). By removing biomass from the system, the stressor would also lower the mass-balance constraint (i.e., $\frac{\partial s}{\partial E} < 0$).

For instance, suppose the dynamics of the consumer species were now given by

$$\frac{dN_i}{N_i dt} = r_i\left[R - R_i^* - \alpha_i P - \gamma_i E\right]; \qquad (30)$$

where $r_i \gamma_i$ is the per-capita, per-unit intensity mortality rate inflicted by the stressor on species i. Suppose also that the mass-balance constraint was affected by the stress, such that there was less biomass in the system (e.g., because of harvesting); i.e., $s = s(E)$ and $s'(E) < 0$. In this case, the equilibrium resource and predator abundances that would be reached with stress ($E > 0$) and only species i (no species j), denoted R_i' and P_i', respectively, are given by

$$R_i' = R_i^{**} + \gamma_i E - \alpha_i \frac{b_P[s(0) - s(E) + \gamma_i E]}{\alpha_i b_P + 1} \qquad (31)$$

$$P_i' = P_i^{**} - \frac{b_P[s(0) - s(E) + \gamma_i E]}{\alpha_i b_P + 1}. \qquad (32)$$

From Eq. (32), we can see that the term $\frac{b_P[s(0) - s(E) + \gamma_i E]}{\alpha_i b_P + 1}$ represents the reduction in equilibrium predator abundance ($P_i^{**} - P_i'$) caused indirectly by the stressor, when species j is not present. Thus, from Eq. (31), the increase in equilibrium resource abundance caused by the stressor ($R_i' - R_i^{**}$), when species j is not present, is the sum of two impacts: the effect of increasing species i's mortality ($\gamma_i E$), which reduces pressure on the resource, and the effect of reducing predator abundance ($\alpha_i \frac{b_P[s(0) - s(E) + \gamma_i E]}{\alpha_i b_P + 1}$), which indirectly increases pressure on the resource.

Thus, defining a sensitivity parameter, v_i, is not as straightforward in this model as in the previous two. Even though the definition of γ_i in Eq. (30) seems analogous to v_i in the previous models, it is not the case where $\gamma_i = \gamma_j$ which implies no effect of stress on coexistence. However, the main model insight regarding weak similarity and broadly inflicted stress is the same: There is still a single special case in which stress does not affect coexistence, namely when $\frac{\partial (R_j' - R_i')}{(R_j' - R_i')\partial E} = \frac{\partial (P_j' - P_i')}{(P_j' - P_i')\partial E}$. This case is analogous to the equal-sensitivity cases in the previous two models. If $\frac{\partial (R_j' - R_i')}{(R_j' - R_i')\partial E} > \frac{\partial (P_j' - P_i')}{(P_j' - P_i')\partial E}$, increasing stress perturbs competition to the disadvantage of species j (the predator specialist), and if $\frac{\partial (R_j' - R_i')}{(R_j' - R_i')\partial E} < \frac{\partial (P_j' - P_i')}{(P_j' - P_i')\partial E}$, increasing stress perturbs competition to the disadvantage of species i (the resource specialist). It is also possible to derive

bounds, analogous to Eqs. (4), (21a), and (21b), on the stressor intensity, E_c, causing competitive exclusion of the more sensitive competitor—the upper bound approaches zero as α_j approaches α_i. For instance, suppose stress disadvantages species i (as in the examples in the previous models), i.e., $\frac{\partial (R_j' - R_i')}{(R_j' - R_i')\partial E} < \frac{\partial (P_j' - P_i')}{(P_j' - P_i')\partial E}$; stress impacts both consumer species as assumed by Eq. (30); $R_j^{**} > R_i^{**}$ and $P_j^{**} > P_i^{**}$; and $s(E) = s_0 - s'E$. Then

$$0 < E_c \leq \frac{(\alpha_j - \alpha_i)(P_j^{**} - P_i^{**})}{\left[(\alpha_i - \alpha_j)\left(\frac{b_P[s' + \gamma_i]}{\alpha_i b_P + 1} - \frac{b_P[s' + \gamma_j]}{\alpha_j b_P + 1}\right) + \gamma_i - \gamma_j\right]}. \qquad (33)$$

The upper bound of E_c approaches zero as the niches approach total similarity (i.e., as α_i approaches α_j).

Model 3: competition-colonization tradeoff

Our third and final mechanistic model (Fig. 3g) is based on that of Calcagno et al. (2006). It explores a competition-colonization tradeoff in which differences between species in local competitive ability are cardinal (i.e., numeric and continuous) rather than ordinal [i.e., ranked, but not continuous; differences in competitive ability are ordinal in earlier competition-colonization models such as those of Levins (1969), Tilman (1994), or Kinzig et al. (1999)]. In this model, abundance is measured in terms of the proportion of total sites in the ecosystem that are occupied by each species, p_i for species i. Two species cannot occupy the same space (i.e., $p_1 + p_2 \leq 1$). Species i attempts to colonize sites that it does not currently occupy at rate c_i; it is always successful when attempting to colonize empty sites. Species i is exterminated from sites it occupies at rate M_i, by a combination of natural processes and the anthropogenic stressor. We define a standardized mortality measure, m_i, which measures mortality as a fraction of the colonization rate ($m_i = M_i/c_i$). When species i attempts to colonize a site in which species j is currently resides, species i has a success rate of displacing species j of $\eta_{i,j}$ ($\eta_{i,j} + \eta_{j,i} = 1$), which is negatively correlated with the differences in colonization rates—i.e., better colonizers (measured by c_i) are worse competitors (measured by $\eta_{i,j}$). The dynamics of species i's site occupancy are given by

$$\frac{dp_i}{dt} = c_i p_i \left(1 - p_i - p_j - m_i + p_j \eta_{i,j} - \frac{c_j}{c_i} p_j \eta_{j,i}\right) \qquad (34)$$

$$\eta_{i,j} = \frac{\omega_i}{\omega_i + \omega_j} \qquad (35)$$

$$\omega_i = \exp(-\beta c_i). \qquad (36)$$

We do not consider preemption competition, as do Calcagno et al. (2006), and thus, we also do not generally find limits to *dis*similarity in our model, as they do.

As in model 2 above, the condition for stable coexistence of the two species in this model is that each species must have positive growth in occupancy ($dp_i/dt > 0$ for species i) when it is rare (when $p_i \approx 0$ for species i) and the other species is at the equilibrium it would reach in the absence of the other species, denoted p_i^{**} for species i. From Eq. (34), single-species equilibrium for species i is (Levins 1969)

$$p_i^{**} = 1 - m_i. \tag{37}$$

Thus, coexistence requires

$$0 < 1 - m_i - p_j^{**} \eta_{j,i} \left(1 + \frac{c_j}{c_i} \right). \tag{38}$$

Equation (38), for both species, can be re-written as

$$\eta_{j,i} \left(1 + \frac{c_j}{c_i} \right) < \frac{1 - m_i}{1 - m_j} < \frac{1}{\left(1 + \frac{c_i}{c_j} \right) \eta_{i,j}}. \tag{39}$$

This condition is analogous to Eqs. (3a), (19), and (29) from the other models, under most parameter values. As the two species become similar in niche (i.e., c_i approaches c_j, implying that $\eta_{j,i}$ and $\eta_{i,j}$ both approach 0.5, and $\eta_{j,i} \left(1 + \frac{c_j}{c_i} \right)$ approaches $\frac{1}{\left(1 + \frac{c_i}{c_j} \right) \eta_{i,j}}$), the range of relative mortality rates ($\frac{1 - m_i}{1 - m_j}$) allowing coexistence becomes smaller (Fig. 3h).

The exception occurs when either c_i or β is relatively small (e.g., $c_i < 0.05$ or $\beta < 20$). In such cases, the competitive disadvantage of species i's lesser colonization ability becomes harder, rather than easier, to offset via better competition (higher $\eta_{i,j}$) as the difference in niche ($\frac{c_j}{c_i}$) magnifies. The reason for this is that lower values of β carry less of a competition advantage per unit decrease in colonization ability. However, assuming that the species coexist with no stress ensures that β has a relatively high lower-bound $\beta > \frac{\log(c_j) - \log(c_i)}{c_j - c_i}$ [by Eq. (39)]. For instance, if $c_1 = 0.2$ and $c_2 = 0.1$, $\beta > 7$. Thus, it is a relatively limited range of intermediate β values under which Eq. (39) does not hold. Note also that the classic competition-colonization model (e.g., Tilman 1994), in which the poorer colonizer always wins in local competition, would be equivalent to $\beta = \infty$ (i.e., $\eta_{i,j} = 1$, $\eta_{j,i} = 0$, when species i is the inferior colonizer, and they make the additional assumption that $m_{i0} c_i = m_{j0} c_j$).

Assuming parameters are such that the range of relative mortality rates decreases as the species become similar in

niche (as in the other models), it is straightforward to show that the stressor intensity causing competitive exclusion of one of the species has an upper bound, which approaches zero as the niches approach identity (i.e., as c_i approaches c_j). For instance, suppose the stressor intensity (E) has a linear effect on the mortality of each species

$$m_i = m_{i0} + \gamma_i E \tag{40}$$

where m_{i0} is the baseline natural mortality for species i. Coexistence Eq. (39) becomes

$$\eta_{j,i} \left(1 + \frac{c_j}{c_i} \right) < \frac{1 - m_{i0} - \gamma_i E}{1 - m_{j0} - \gamma_j E} < \frac{1}{\left(1 + \frac{c_i}{c_j} \right) \eta_{i,j}}. \tag{41}$$

If $\gamma_i = \left(\frac{1 - m_{i0}}{1 - m_{j0}} \right) \gamma_j$, $\frac{1 - m_{i0} - \gamma_i E}{1 - m_{j0} - \gamma_j E}$ does not change as E increases—this is the equal sensitivity scenario. If $\gamma_i > \left(\frac{1 - m_{i0}}{1 - m_{j0}} \right) \gamma_j$, stress competitively disadvantages species i and the intensity (E_c) needed to competitively exclude species i is bounded by

$$0 < E_c \le \frac{(1 - m_{i0}) \left(1 - \eta_{j,i} \eta_{i,j} \left(2 + \frac{c_j}{c_i} + \frac{c_i}{c_j} \right) \right)}{\left(\gamma_i - \eta_{j,i} \left(1 + \frac{c_j}{c_i} \right) \gamma_j \right)}. \tag{42}$$

These bounds are analogous to Eqs. (4), (21a), (21b), and (33) in the other three models. As c_i approaches c_j, $\eta_{i,j}$ and $\eta_{j,i}$ approach 0.5. Thus, $1 - \eta_{j,i} \eta_{i,j} \left(2 + \frac{c_j}{c_i} + \frac{c_i}{c_j} \right)$ approaches zero, as does the upper bound on E_c.

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