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Differences among species in seed dispersal and conspecific neighbor effects can interact to influence coexistence

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Abstract

Seed dispersal is a critical mechanism for escaping specialist natural enemies. Despite this, mean dispersal distances can vary by an order of magnitude among plant species in the same community. Here, we develop a theoretical model to explore how interspecific differences in seed dispersal alter the impact of specialist natural enemies, both on their own and though a trade-off between seed dispersal and enemy susceptibility. Our model suggests that species are more able to recover from rarity if they have high dispersal because (1) seedlings are more likely to escape their parent's natural enemies, (2) adults are more spread out, reducing the chance that a seed will disperse near conspecifics, and (3) seedlings compete less with kin for open gaps. Differences in dispersal do not produce stabilizing mechanisms—species with low dispersal are purely at a disadvantage and do not gain a novel niche opportunity. However, dispersal-susceptibility trade-offs will be equalizing, as species disadvantaged by low dispersal will benefit from being less susceptible to specialist natural enemies. This mechanism, unlike most mechanisms of dispersal-mediated coexistence, does not require that there is an abundance of empty space: high-dispersers gain an advantage by escaping from their enemies, not by colonizing empty habitat. Our study therefore suggests that differences in dispersal are unlikely to promote diversity on their own, but may strengthen other coexistence mechanisms.

Keywords Janzen-Connell hypothesis · Plant-soil feedback · Modern coexistence theory · Apparent competition · Seed dispersal · Natural enemies

Introduction

Tropical forests contain hundreds of tree species, far more than the number of limiting resources, and how this can occur has long puzzled ecologists (Hutchinson 1961). Specialist natural enemies (e.g., pathogens, herbivores, and seed predators) are thought to drive coexistence, as species that become rare will have increased recruitment due to a lack of natural enemies (Gillett 1962; Janzen 1970; Connell 1971). Specialist natural enemies are thought to be common (Terborgh 2012; Comita et al. 2014), and non-spatial models suggest they could be a powerful mechanism promoting diversity (Grover 1994; Bever et al. 1997). However, specialist natural enemies are not homogeneously distributed across communities; instead, many are distance-responsive (occurring near adult hosts) or density-responsive (occurring in areas of high seedling density) (Janzen 1970). Similarly, seeds are not homogeneously distributed; instead, many disperse within a few dozen meters of their parent (Muller-Landau 2008; Bullock et al. 2017). Recent studies have shown that these spatial effects matter. Distance-responsive enemies are less effective at promoting coexistence, because if a species becomes rare, and its seeds mostly stay in high-mortality zones due to limited dispersal, then it will still experience high mortality (Stump and Chesson 2015). Also, if tree species differ in susceptibility to their natural enemies (as they do in many plant communities (Klironomos 2002; Mangan et al. 2010; Zhu et al. 2018; Chen et al. 2019)), then species that are more susceptible will tend to be less abundant and potentially excluded from the community (Mangan et al. 2010; Chisholm and Muller-Landau 2011;

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Miranda et al. 2015; Stump and Comita 2018). Exclusion occurs because limited dispersal ensures that many seeds are exposed to their parent's natural enemies; therefore, tree species that are highly susceptible to those natural enemies are at a disadvantage (Stump and Comita 2018). Thus, understanding how seed dispersal interacts with distance- and density-responsive enemies is critical for understanding how (or if) specialist natural enemies promote diversity.

Nearly every model of distance-responsive enemies makes the simplifying assumption that tree species have equal dispersal (e.g., Adler and Muller-Landau (2005), Mangan et al. (2010), Sedio and Ostling (2013), Stump and Comita (2018), and Levi et al. (2019)). In reality, co-occurring tree species can have mean dispersal distances that vary by an order of magnitude (Muller-Landau 2008), and this will likely alter plant interactions. Species with high dispersal have an advantage in spatially homogeneous environments (Hastings 1980) and a disadvantage in spatially heterogeneous environments (Hastings 1983; Snyder and Adler 2011). Numerous models have shown competition-dispersal trade-offs can allow species to coexist (Hastings 1980; Bolker and Pacala 1999; Yu and Wilson 2001) and may boost the ability of other mechanisms to promote diversity (Gross 2008). Also, in a recent theoretical study, we showed that differential susceptibility to natural enemies could undermine diversity; however, our model also revealed that if there was an equalizing trade-off, such that susceptible species had some competitive advantage, then differential susceptibility could promote diversity (Stump and Comita 2018). We believe that a dispersal-susceptibility trade-off could produce such an equalizing effect.

It has long been hypothesized that seed dispersal and enemy susceptibility will trade off (Howe 1993). Smaller seeds are more susceptible to natural enemies (Lebrija-Trejos et al. 2016; Clark et al. 2018), and there is some evidence that smaller seeds disperse farther ((Muller-Landau 2008), but see Seidler and Plotkin (2006) and Clark et al. (2018)). Dispersal-susceptibility trade-offs are likely related to tree species life history strategies. Specifically, species on the fast end of the fast-slow life history continuum—i.e., those that invest in growth and reproduction over maintenance—tend to have higher seed dispersal than those on the slow end of the continuum (Beckman et al. 2018); such "fast" species also tend to invest less into defense (Loehle 1988) and thus be more susceptible to natural enemies. Finally, this trade-off seems likely to evolve—species that are highly susceptible to distance-responsive enemies will be under stronger selection to increase seed dispersal (Howe and Smallwood 1982).

The spatial distribution of adults likely alters the impact of natural enemies. Species with low seed dispersal tend to be more clustered (Seidler and Plotkin 2006), and therefore, their seeds likely experience high mortality even if they are rare on the landscape (Fricke and Wright 2017). Additionally, rare species tend to be more clustered than common ones (Condit et al. 2000), though it is not clear if this is a cause or consequence of rarity. Despite this, the exact impact of spatial structure on distance- and density-responsive enemies is unknown. All studies that we are aware of either used a spatially implicit approach that does not produce spatial structure (e.g., Bever et al. (1997) and Stump and Chesson (2015)) or used simulations that did not tease apart the impact of clustering from other effects (e.g., Muller-Landau and Adler (2007) and Mack and Bever (2014)). Thus, it is not clear if spatial structure alters stabilizing mechanisms or reduces the fitness of species that are more clustered.

We developed a spatially explicit model designed to address the following questions:

- How do interspecific differences in seed dispersal affect stabilizing mechanisms and fitness effects, both on their own and through interactions with specialist natural enemies?
- What impact does the spatial aggregation of adults have on coexistence, and how are its effects altered by differences in seed dispersal and enemy susceptibility?

Using a hybrid approach of computer simulations and analysis, we found that spatial structure weakens stability, as rare species become clustered and therefore more exposed to natural enemies. Species with high dispersal gain three advantages: seeds are likely to escape their parent's natural enemies, adults are less clustered, and seeds experience less competition from kin. On their own, these undermine coexistence by creating fitness differences. However, we found that dispersal-susceptibility trade-offs have an equalizing effect, which makes it easier for coexistence in the presence of specialist natural enemies. Our results also produce a general method for analyzing future simulations of distance- and density-responsive enemies and reveal key variables to measure in future empirical studies.

Methods

We modeled competition between R tree species (Fig. 1). Variables and parameters are listed in Table 1. The forest is an $L \times L$ grid of sites. Each site is an $l \times l$ square containing one adult. We define $N_j(x,t)$ as 1 if a species j adult occupies site x at time t, and 0 otherwise; $\mathbf{E}\left[N_j(t)\right]$ is the fraction of sites held by species j at time t.

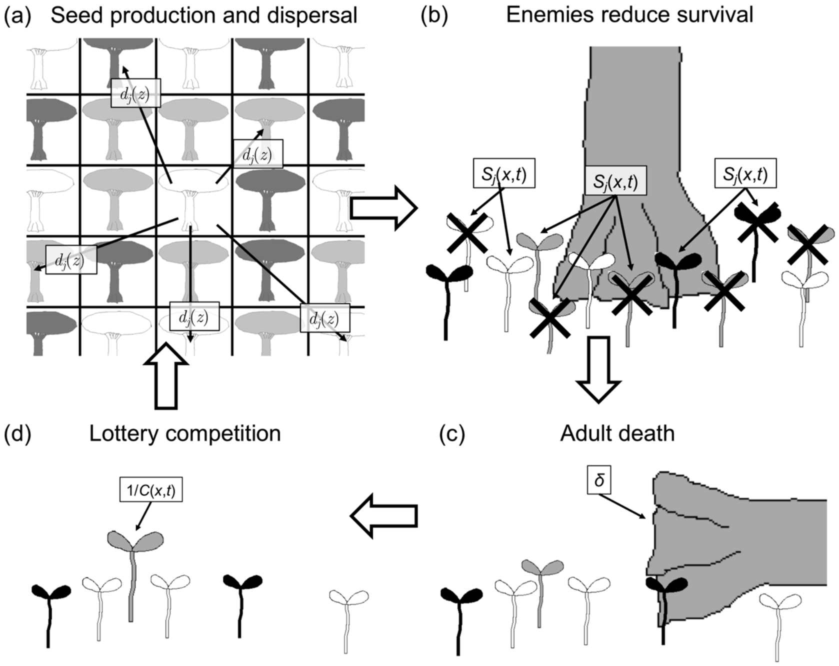

Fig. 1 A diagram of our model. We modeled the life of a tree in four steps. **a** First, each adult produces Y_j seeds (for species j) and disperses them according to its dispersal kernel, $d_j(z)$. **b** Second, seedlings are exposed to natural enemies. Each survives with probability $S_j(x,t)$ (for species j, at site x and time t), which is reduced by nearby adult conspecifics and conspecific seedlings in the same site. **c** Third, each adult dies with probability δ. If the adult survives, the seeds under it die. **d** If the adult dies, the $C(x,t)$ seedlings at the site compete to capture the site

In the model, four processes occur each time step (Fig. 1). First, each adult produces Y_j seeds (for sp. j) and disperses them according to its dispersal kernel $d_j(z)$ (where $d_j(z)$ is the probability a seed of species j disperses to a site a given site a distance z away). Second, seeds survive the seed-to-seedling transition with probability $S_j(x,t)$ (for sp. j at site x and time t). Third, each adult dies with density-independent probability δ. If the adult lives, the seedlings under it die. Last, if an adult dies, then a random seedling present at the site becomes the adult by the next time step;

Table 1 Parameters, variables, and functions used in our model

Parameter	Description
I_j	Baseline (density-independent) probability of seedling survival for species j
$p_{\mathrm{A},j}$	Potential negative density dependence cause by distance-responsive enemies (sp. j) (A for the impact of adults)
$p_{\mathrm{S},j}$	Potential negative density dependence caused by density-responsive enemies (sp. j) (S for the impact of seeds)
Y_j	Number of seeds produced by each adult of species j each time step
δ	Probability an adult will die each time step
L	Length of the community (in number of adults)
l	Length of a site
R	Number of competing species
Variable	Description
p_j	Potential negative density dependence for sp. j (the combined effect of distance- and density-responsive enemies) (Eq. 3)
$\mathbf{E}\left[N_j(t)\right]$	Frequency of species j
$N_j(x,t)$	Occupancy variable for species j at site x at time t
Function	Description
$d_j(z)$	Seed dispersal kernel for species j (the probability a seed disperses a distance z)
$d_{\mathrm{A},j}(z)$	Distribution kernel for distance-responsive enemies of species j (the distribution of enemies at distance z)
$d_{\mathrm{p}-j}(z)$	Distribution kernel for enemies of species j (the distribution of enemies at distance z, Eq. 4)
$\lambda_j(x,t)$	Fitness of an adult of species j at site x at time t, (Eq. 1)
$\tilde{\lambda}'_j(t)$	Growth rate of species j (i.e., mean of $(\lambda_j(x,t)-1)/\delta$ over all adults, Eq. 31)
$S_j(x,t)$	Probability a sp. j seed survives to become a seedling (site x time t), (Eq. 2, 5)
$C(x,t)$	Total number of seedlings competing for site x at time t (Eq. 21)
$\widetilde{d_j d_{\mathrm{P},j}}$	The product of the seed and natural enemy dispersal kernels for species j, summed over all sites (i.e. their dot product, Eq. 33)

thus, if there are a total of $C(x,t)$ seedlings at site x, then each has a $1/C(x,t)$ chance of becoming an adult. Therefore, a sp. j adult at x will disperse $Y_j d_j(|x-y|)$ seeds to a given site y (where $|x-y|$ is the distance between x and y), and each will become an adult with probability $\delta S_j(y,t)/C(y,t)$. The expected fitness of an adult, $\lambda_j(x,t)$ (for species j adult site x and time t), is the chance it survives plus the expected number of adults it will produce by the next time step (i.e., the probability of recruitment summed over all sites),

$$\lambda_j(x,t) = (1-\delta) + Y_j \sum_{y=1}^{L^2} d_j(|x-y|)\delta \frac{S_j(y,t)}{C(y,t)}, \tag{1}$$

where the summation is across all sites. The growth rate of species j, $\tilde{\lambda}'_j(t)$, is then the mean of $\lambda_j(x,t)$ over all sites containing a species j adult. We derive $\tilde{\lambda}'_j(t)$ in Appendix A1 (Eq. 31).

The dispersal kernel $d_j(z)$ must sum to 1 across all sites. We assume that dispersal is only affected by distance, such that the probability of a seed dispersing from x_1 to y_1 is the same as the probability of dispersing a seed from x_2 to y_2 as long as $|x_1-y_1| = |x_2-y_2|$. However, $d_j(z)$ can take on any form (we chose a specific form for computer simulations, see below).

We assume that each seedling has a baseline chance I_j of survival (for sp. j), which is reduced by nearby conspecifics. We define $p_{\mathrm{A},j}$ and $p_{\mathrm{S},j}$ as the potential negative density dependence (NDD) caused by distance- and density-responsive enemies (the maximum effect they can have on mortality, Kobe and Vriesendorp (2011)), respectively. Each conspecific adult z sites away reduces survival by $p_{\mathrm{A},j} d_{\mathrm{A},j}(z)$ (where $d_{\mathrm{A},j}(z)$ is the distribution kernel of enemies produced in x). Each conspecific seed at the site reduces survival by $p_{\mathrm{S},j}/Y_j$. There will be $\sum_{y=1}^{L^2} Y_j d_j(|y-x|)N_j(y,t)$ seeds of sp. j that disperse to x at time t (summed over all y sites). Thus, the chance of surviving the seed-to-seedling transition is

$$S_j(x,t) = I_j \left(1 - \sum_{y=1}^{L^2} p_{\mathrm{A},j} d_{\mathrm{A},j}(|y-x|) N_j(y,t) - \sum_{y=1}^{L^2} Y_j p_{\mathrm{S},j} d_j(|y-x|) N_j(y,t)\right), \tag{2}$$

(where the summations are over all y sites). Thus, the first summation is the impact of distance-responsive enemies, and the second is the impact of density-responsive enemies. We assume that the parameters are constrained such that $S_j(x,t) \geq 0$. Our results also work if $S_j(x,t)$ is approximately a linear function of enemy density (Appendix A1.2).

Equation 2 can be simplified by combining the natural enemy terms. We do this by defining a combined potential NDD as

$$p_j = p_{\mathrm{A},j} + p_{\mathrm{S},j} \tag{3}$$

and a combined enemy distribution kernel as

$$d_{\mathrm{p}-j}(z) = \frac{p_{\mathrm{A},j} d_{\mathrm{A},j}(z) + p_{\mathrm{S},j} d_j(z)}{p_j}. \tag{4}$$

Under these definitions, survival becomes

$$S_j(x,t) = I_j \left(1 - \sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}(|y-x|) N_j(y,t)\right). \tag{5}$$

Thus, distance- and density-responsive enemies have equivalent effects on coexistence, as density-responsive enemies are essentially distance-responsive enemies whose distribution kernel matches its host's seed dispersal kernel.

Model analysis

We analyzed our model with invasion analysis (Turelli 1978). Each species was selected in turn to be an invader (denoted with subscript i) and removed from the community. The other species (the residents, subscript r) grew to equilibrium and reached a stable spatial structure. Then, a small number of invaders were introduced into the community randomly. They were given some time to reach a stable spatial structure, and then we measured their population-level growth rate, $\tilde{\lambda}'_i$. If every species had a positive invader growth rate, they coexisted (Turelli 1978).

To quantify what factors allowed species to coexist, we partitioned each species' growth rate into six components, using methods in Barabás et al. (2018) and Chesson (2000). We compared the invader's value of each component to that of the average resident (Chesson 2000). If the invader's value was more positive, it indicates that the species had an advantage, helping it invade. We calculated the stabilizing effect of a component by averaging this invader-resident difference across species (Chesson 2003; Barabás et al. 2018). If this number was positive, it helped species to coexist; if it was negative, it undermined coexistence. Additionally, we calculated the fitness effect of each component on species j by taking species j's invader-resident difference and subtracting the stabilizing mechanism (Chesson 2003; Barabás et al. 2018). If this value is positive, it indicates that the mechanism gives species j a competitive advantage overall.

Most of the work was done analytically (Appendix A1, A2). However, population dynamics were affected by how aggregated each species was, and we could not predict this from our parameters. Instead, we analyzed the impact of the spatial structure by comparing computer simulations to an analytical approximation that lacked spatial structure

(Stump et al. 2018a) (Appendix A4). We also used simulations to test how a species' dispersal distance and frequency affected its spatial distribution (Appendix A5). To speed computation, we determine the distance between sites using the Manhattan distance function (i.e., the distance between sites (x_1, y_1) and (x_2, y_2) is $|x_1 - x_2| + |y_1 - y_2|$, Appendix A3). We simulated dispersal using a discrete approximation of a 2-dimensional t (2Dt) distribution (Clark et al. 1999; Muller-Landau 2008), modeled natural enemy distribution with a negative exponential function (Comita et al. 2010), and assumed that the log-likelihood of survival was a linear function of potential NDD; we explain how each of these were implemented in Appendix A3 (specifically, Eqs. 73 and 74 for dispersal, Eq. 57 for enemy distribution, and Eq. 75 for seedling survival). We simulated the model using Matlab 2017b (The MathWorks Inc 2017) and 2019a (The MathWorks Inc 2019), using code that was modified from previous work (Stump et al. 2018b; Stump and Comita 2018).

Throughout the text, we use $\mathbf{E}[A]$ to indicate the spatial average of A over all sites x, $\overline{A}$ to indicate an average of A over species, $\mathbf{cov}\,(A, B)$ to indicate a covariance between A and B over all sites y, and $\mathbf{cov}^{\mathrm{S}}\,(A, B)$ to indicate a covariance of A and B over species. We will use the summation $\sum_{y=1}^{L^2}$ to indicate a sum over all sites y, the sum $\sum\limits_{r \neq i}$ to indicate a sum over all residents species r, and $\sum_{j=1}^{R}$ to indicate a sum over all species j.

Results

We partitioned invader growth rates into six factors (Table 2), such that the growth rate of an invader can be written as

$$\frac{\tilde{\lambda}_i - 1}{\delta} \approx \Delta Y_i + \Delta P_i + \Delta\kappa_{\mathrm{P}i} + \Delta\kappa_{\mathrm{C}i} + \Delta\kappa'_{\mathrm{P}i} + \Delta\kappa'_{\mathrm{C}i}. \quad (6)$$

Each Δ term represents a comparison between the invader and the residents in some factor that affects their fitness; we will discuss each term in detail below. We found approximations for the first four factors that closely matched simulations (Figs. 7 and 8). We could not approximate the last two terms because they depended on the spatial structure of the community and therefore could only be measured using simulations. Most quantities in Table 2 can be measured empirically; we describe how to do so in the "Discussion."

We present three scenarios for how differences in dispersal affect coexistence. As a baseline, we first examine a community where species have identical dispersal and susceptibility to natural enemies. Second, we examine how the model changes if species have different mean dispersal distances. Third, we examine how it changes if species differ in both seed dispersal and susceptibility to natural enemies.

Baseline: no difference in dispersal or susceptibility

Our model was designed so that species have an advantage if they produce more seeds, or if those seeds have higher survival. This effect is quantified by the term ΔY_j,

$$\Delta Y_i = \frac{R}{R-1}\left(\ln\{Y_i I_i\} - \overline{\ln\left\{Y_j I_j\right\}}\right) \quad (7)$$

where $\overline{\ln\left\{Y_j I_j\right\}}$ is the across-species mean of the product of Y_j (the number of seed produced each time step) and I_j (density-independent survival). The mean of $\ln\{Y_i I_i\} - \overline{\ln\left\{Y_j I_j\right\}}$ across species is 0; therefore, this term produces only fitness-differences. If species with high Y_j have low I_j, this can create an equalizing trade-off, but it cannot create any novel niche interactions. Thus, in the absence of a rare species advantage, the species with the highest ΔY_j will dominate.

We found that rare species gain an advantage because their specialist natural enemies are also rare. This effect can be quantified by calculating the mean chance a seed would die in a random site (and comparing residents vs. invaders):

$$\begin{aligned}\Delta P_i &= -\mathbf{E}\left[\sum_{y=1}^{L^2} p_i d_{\mathrm{p}-i}\left(|y-x|\right) N_i(y,t)\right] \\ &\quad + \frac{1}{R-1}\sum_{r\neq i}\mathbf{E}\left[\sum_{y=1}^{L^2} p_r d_{\mathrm{p}-r}\left(|y-x|\right) N_r(y,t)\right], \quad (8)\end{aligned}$$

(Appendix A1). When species have identical dispersal and natural enemy susceptibility (i.e., $p_j = \overline{p_j}$ for all j), then this can be approximated as

$$\Delta P_i \approx \frac{\overline{p_j}}{R-1}. \quad (9)$$

This will be identical between species, and thus stabilizing: the rarer a species is, the less likely a seed is to encounter distance- or density-dependent enemies, and thus, the more likely it is to survive. The stabilizing term is proportional to $\overline{p_j}$, because the more harmful natural enemies are, the more a species benefits if its natural enemies become rare.

Of course, seeds are not randomly distributed across the landscape, and our model revealed that spatial structure has two effects that weaken the stabilizing impact of natural enemies. First, seeds tend to fall near their parent and thus may be killed by their parent's distance-responsive enemies,

Table 2 A list of factors affecting invader growth rates. The approximations are listed in units of increased fitness per lifetime, $\tilde{\lambda}'_j(t)$. An overline indicates the mean across all species, and the covariance is over all species at equilibrium

Description	Stabilizing mechanism	Fitness difference
Effect of seed yield and density-independent seedling survival ΔY_j	$\overline{\Delta Y} = 0$ **Zero**.	$\Delta Y_j - \overline{\Delta Y} = \frac{R}{R-1}\left(\ln\left\{Y_j I_j\right\} - \overline{\ln\{Y_r I_r\}}\right)$ **Positive** if species j has above-average seed yield and seedling survival.
Mean effect of natural enemies, ΔP_j	$\overline{\Delta P} \approx \frac{\overline{p_j}}{R-1} + \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}\left[N_j(t)\right], p_j\right)$ **Positive** (unless there is positive density dependence).	$\Delta P_j - \overline{\Delta P} \approx \frac{-p_j+\overline{p_j}}{(R-1)^2}$ Very small, **positive** for species that tolerate natural enemies.
Effect of parent's natural enemies, $\Delta\kappa_{\mathrm{P}j}$	$\overline{\Delta\kappa_{\mathrm{P}}} \approx \frac{\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}}{R-1} - \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}\left[N_j(t)\right], p_j \widetilde{d_j d_{\mathrm{P},j}}\right)$ **Negative**.	$\Delta\kappa_{\mathrm{P}j} - \overline{\Delta\kappa_{\mathrm{P}}} \approx -\frac{R}{R-1}\left(p_j \widetilde{d_j d_{\mathrm{P},j}} - \overline{p_r \widetilde{d_r d_{\mathrm{P},r}}}\right)$ **Positive** for species that can tolerate or disperse away from their natural enemies.
Effect of parent competition, $\Delta\kappa'_{\mathrm{C}j}$	No approximation **Negative**.	No approximation **Positive** for species that are less aggregated (likely those with high seed dispersal).
Spatial structure of natural enemies, $\Delta\kappa_{\mathrm{C}j}$	Approximation in Appendix A2.4 (Eqs. 59 and 66) **Negative**, but smaller than $\overline{\Delta P}$ and $\overline{\Delta\kappa_{\mathrm{P}}}$	Approximation in Appendix A2.4 (Eqs. 59 and 66) **Positive** for species with high dispersal
Spatial structure of competition, $\Delta\kappa'_{\mathrm{C}j}$	No approximation **Negative**.	No approximation **Positive** for species with high dispersal.

or density-responsive enemies generated by kin. We can quantify the impact that a parent has on its offspring as

$$\begin{aligned}\Delta\kappa_{\mathrm{P}i} &= L^2\mathbf{E}[\mathbf{cov}\,(d_i(|x-y|), \ln\{S_i(y,t)\})] \\ &\quad - \frac{L^2}{R-1}\sum_{r\neq i}\mathbf{E}[\mathbf{cov}\,(d_r(|x-y|), \ln\{S_r(y,t)\})] \qquad (10)\end{aligned}$$

where the covariance is over all sites x (Appendix A2.5). When p_j and $d_j(|x-y|)$ are identical for species, Eq. 10 can be simplified. To do this, we must calculate the chance that a seed encounters a natural enemy produced bit its kin, it is the dot product of $d_j(z)$ (sp. j's seed dispersal kernel) and $d_{\mathrm{P}-j}(z)$ (sp. j's enemy distribution kernel) (i.e., the sum of their product over all sites), which we will call $\widetilde{d_j d_{\mathrm{P},j}}$. Thus, if p_j and $d_j(z)$ are identical for species, Eq. 10 can be approximated as

$$\Delta\kappa_{\mathrm{P}i} \approx \frac{-\overline{p_j}\,\overline{\widetilde{d_j d_{\mathrm{P},j}}}}{R-1} \qquad (11)$$

where $\overline{\widetilde{d_j d_{\mathrm{P},j}}}$ is the mean of $\widetilde{d_j d_{\mathrm{P},j}}$ over species (Appendix A2.3). $\overline{p_j}$ and $\widetilde{d_j d_{\mathrm{P},j}}$ are strictly positive; thus, $\Delta\kappa_{\mathrm{P}i}$ produces a negative stabilizing mechanism (Fig. 2c). Essentially, the impact of a parent's seeds on its offspring represent a density-independent effect, and thus, those seeds will not generate a stabilizing mechanism. This term thus removes some of the rare-species advantage generated by ΔP_i. This term will approach 0 if either seeds or natural enemies are spread out across the landscape.

Second, we found that species are harmed if they are spatially clustered, because seeds are more likely to disperse near a conspecific and therefore encounter natural enemies. This effect can be quantified as

$$\begin{aligned}\Delta\kappa'_{\mathrm{P}i} &= L^2\mathbf{cov}\left(\mathbf{cov}\,(d_i(|x-y|), \ln\{S_i(y,t)\}), \frac{N_i(x,t)}{\mathbf{E}[N_i(t)]}\right) \\ &\quad - \frac{L^2}{R-1}\sum_{r\neq i}\mathbf{cov}\left(\mathbf{cov}\,(d_r(|x-y|), \ln\{S_r(y,t)\}), \frac{N_r(x,t)}{\mathbf{E}[N_r(t)]}\right) \qquad (12)\end{aligned}$$

(where the outer covariance is over sites x, and the inner covariance is over sites y) (Appendix A1.3). Here, the inner covariance chooses a site x and measures the relationship between the chance a seed disperses to a nearby site and log seedling survival that site (this will be positive if sites near that adult have high survival). The outer covariance measures the relationship between the inner covariance at a given site x and the probability that that site will be occupied (this will be positive if adults are more likely to be found in high-survival areas). We could not find an approximation for this, as it would require being able to predict the spatial structure of the adult community from our parameters. However, we could study it using simulations (Appendix A2 and A5). We found that the outer covariance terms in $\Delta\kappa'_{\mathrm{P}j}$ are related to the pair correlation function of adult density (Fig. 10). We also found that $\Delta\kappa'_{\mathrm{P}j}$ is generally negative (Fig. 2e), as the rarer a species is, the

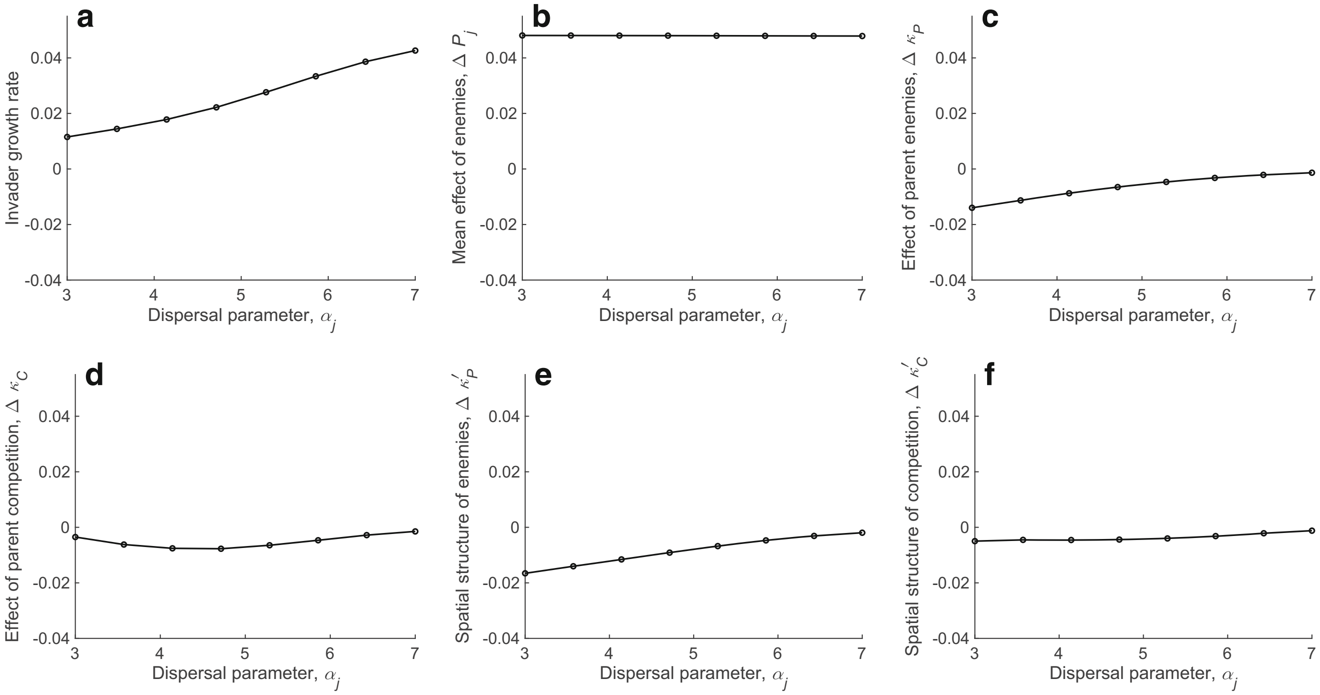

Fig. 2 We simulated an invasion analysis where every species was identical, and showed how stabilizing mechanisms changed as dispersal changed. **a** We show the community average stabilizing mechanism in each community. **b**–**f** We show the Δ mechanisms for each species (excluding ΔY_j). The more positive it is, the stronger contribution it makes to the stabilizing mechanism. We used the following parameters: $S = 7$, $p_{\mathrm{A},j} = 0.3$, $p_{\mathrm{S},j} = 0$, $Y_j = 7.8$, $\delta = 0.4$, $l = 10$, $L = 200$. We modeled dispersal using an approximation of the 2Dt distribution, and α_j is the shape parameter (described in Appendix A3)

more clustered it tends to be across the landscape (Fig. 3). Thus, $\Delta\kappa'_{\mathrm{P}j}$ weakens the stabilizing mechanism: species that are rare on the landscape will continue to experience high seed mortality if most of their seeds remain in an area where they are locally common.

Finally, we found that the number of seeds that die from natural enemies affects the number of seedlings competing for a gap. A site held by a common species will contain a large number of conspecific seedlings, all of which will experience a high chance of enemy-induced mortality. However, a seed that survives its natural enemies will have fewer seedling to compete with, which slightly counteracts the negative effects of natural enemies. The same cannot be said for rare species: if a rare species' seed survives near a conspecific, it is likely to be competing with many heterospecific seedlings. We found that this slightly counteracts ΔP_j. Also, trees with high seed production and survival tend to be surrounded by more seedlings, which slightly offsets the impact of ΔY_j. We quantified these effects as the effect of a parent on nearby seedling competition

$$\begin{aligned}\Delta\kappa_{\mathrm{C}i} &\approx -L^2\mathbf{E}[\mathbf{cov}\left(d_i(|y-x|), \ln\{C(y,t)\}\right)]\\ &+ \frac{1}{R-1}\sum_{r\neq i} L^2\mathbf{E}[\mathbf{cov}\left(d_r(|y-x|), \ln\{C(y,t)\}\right)]. \qquad (13)\end{aligned}$$

(analogous to $\Delta\kappa_{\mathrm{P}j}$, see Appendix A2.4 for its approximation), and the impact of clustering on seedling competition

$$\begin{aligned}\Delta\kappa'_{\mathrm{C}i} &= -L^2\mathbf{cov}\left(\mathbf{cov}\left(d_i(|y-x|), \ln\{C(y,t)\}\right), \frac{N_i(x,t)}{\mathbf{E}[N_i(t)]}\right)\\ &+ \frac{L^2}{R-1}\sum_{r\neq i}\mathbf{cov}\left(\mathbf{cov}\left(d_r(|y-x|), \ln\{C(y,t)\}\right), \frac{N_r(x,t)}{\mathbf{E}[N_r(t)]}\right). \qquad (14)\end{aligned}$$

(where the outer covariance is over all sites x, analogous to $\Delta\kappa'_{\mathrm{P}i}$, Appendix A1.3). When p_j and $d_j(z)$ are identical between species, $\Delta\kappa_{\mathrm{C}i}$ and $\Delta\kappa'_{\mathrm{C}i}$ appear to have little effect (Fig. 2d, f).

Species differ in dispersal

Next, we examine the case where species differ in seed dispersal ($d_j(z)$) but are equally susceptible to natural enemies ($p_j = \overline{p_j}$). In this model, Eqs. 7, 8, 10, 12, 13, and 14 continue to apply, though their approximations will differ.

We found that if species differ in dispersal, then the approximation for mean effect of natural enemies over all sites (ΔP_j) can continue to be approximated by Eq. 9. This occurs because ΔP_j is the mean chance a seedling will die in a random site across the environment. As such, ΔP_j will not differ between species (Fig. 4b).

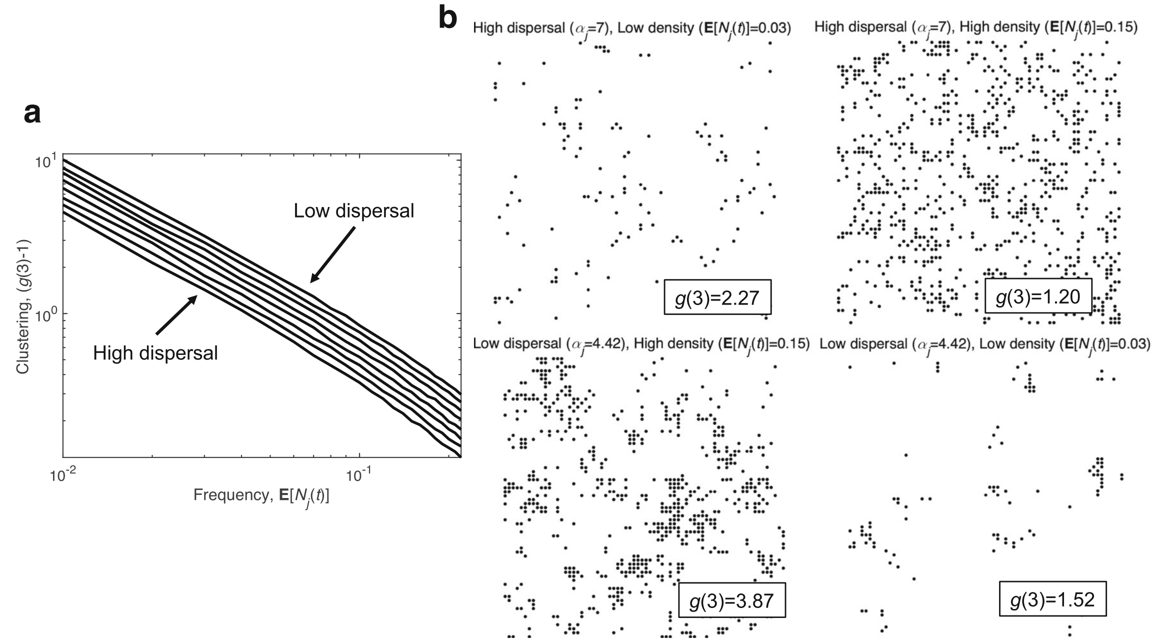

Fig. 3 Species are more clustered when they have low dispersal, and when they are rare. **a** We simulated community dynamics in an 8-species community and calculated the spatial clustering (pair correlation at 3 sites, or 30 m, using Manhattan distances) for each species when it was held at a particular abundance. The pair correlation $g(z)$ is the mean fraction of sites that are occupied by a conspecific a distance z from each adult, divided by the global average frequency; it will be 1 if a species is randomly distributed, and >1 if a species is clustered. Species tended to become more clustered when they become rare. At a given abundance, species with low dispersal tend to be more clustered than those with high dispersal. **b** We show the spatial distribution of the best disperser (mean dispersal 47.6 m, where each site is 10 m × 10 m) when its abundance was held at $\mathbf{E}[N_j(t)] = 0.03$ and 0.15. As it becomes rare, its clustering increases from $g(3) = 1.20$ to 2.27. We also show the spatial distribution of the worst disperser (mean dispersal 14.0m) when its abundance was held at $\mathbf{E}[N_j(t)] = 0.03$ and 0.15. As it becomes rare, its clustering increases from $g(3) = 1.52$ to 3.87. Parameters: $\delta = 0.4$, $l = 10$, $Y_j = 7.8$ for all j, $I_j = 0.269$ for all j, $p_j^A = p_j^S = (0.475, 0.421, 0.368, 0.314, 0.261, 0.207, 0.154, 0.100)$, $d_j(z)$ used a 2Dt distribution with dispersal parameter $\alpha_j = (7, 6.63, 6.26, 5.89, 5.53, 5.56, 4.79, 4.42)$

Instead, we found that differences in dispersal alter the impact of natural enemies by changing the chance a seed will land in a high-mortality site (Fig. 4c). If a species has high dispersal, its seeds are more likely to escape natural enemies generated by its parent; as such, the $\Delta\kappa_{\mathrm{P}i}$ can now be approximated as

$$\Delta\kappa_{\mathrm{P}i} \approx \frac{-\overline{p_j}\overline{\widetilde{d_j d_{\mathrm{P},j}}}}{R-1} - \overline{p_j}\mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)], \widetilde{d_j d_{\mathrm{P},j}}\right) - \frac{R}{R-1}\left(p_i \widetilde{d_i d_{\mathrm{P},i}} - \overline{p\widetilde{d_j d_{\mathrm{P},j}}}\right) \tag{15}$$

(Appendix A2.3). This equation contains two terms that did not appear in Eq. 11. First, the term $\overline{p_j}\mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)], \widetilde{d_j d_{\mathrm{P},j}}\right)$ affects the stabilizing mechanism. It will be negative if the most common species have higher dispersal—in this case, the most common species are also the least regulated by natural enemies, which has previously been shown to weaken the stabilizing mechanism (Stump and Comita 2018). Second, the term $\frac{R}{R-1}\overline{p_j}\left(\widetilde{d_i d_{\mathrm{P},i}} - \overline{\widetilde{d_j d_{\mathrm{P},j}}}\right)$ creates a fitness-difference (Fig. 4c). The term quantifies the difference in the impact a parent tree has on its offspring's chance of enemy-induced mortality. This impact is density-independent; thus, species that have low seed dispersal (and therefore $\widetilde{d_j d_{\mathrm{P},j}}$) are at a density-independent disadvantage against species with a high seed dispersal. When this difference is large between species, it can cause species with high $\widetilde{d_j d_{\mathrm{P},j}}$ to be excluded by species with low $\widetilde{d_j d_{\mathrm{P},j}}$.

Additionally, when species differ in dispersal, they become differently clustered around the landscape. If a species is more spread out, then so too are their specialist natural enemies, weakening their impact. As a result, $\Delta\kappa_{\mathrm{P}j}$ now creates a mean-fitness differences, putting species that are more clustered at a disadvantage (Fig. 4d). Simulations show that species with high seed dispersal were less clustered (Fig. 3); thus, a seed that falls near its parent is less likely to be near a large number of conspecifics (increasing $\Delta\kappa'_{\mathrm{P}i}$).

The new impacts of $\Delta\kappa_{\mathrm{P}i}$ and $\Delta\kappa'_{\mathrm{P}i}$ are slightly reduced by the impact of competition—the more seeds are killed, the lower seedling competition will be (affecting $\Delta\kappa_{\mathrm{C}i}$ and $\Delta\kappa'_{\mathrm{C}i}$).

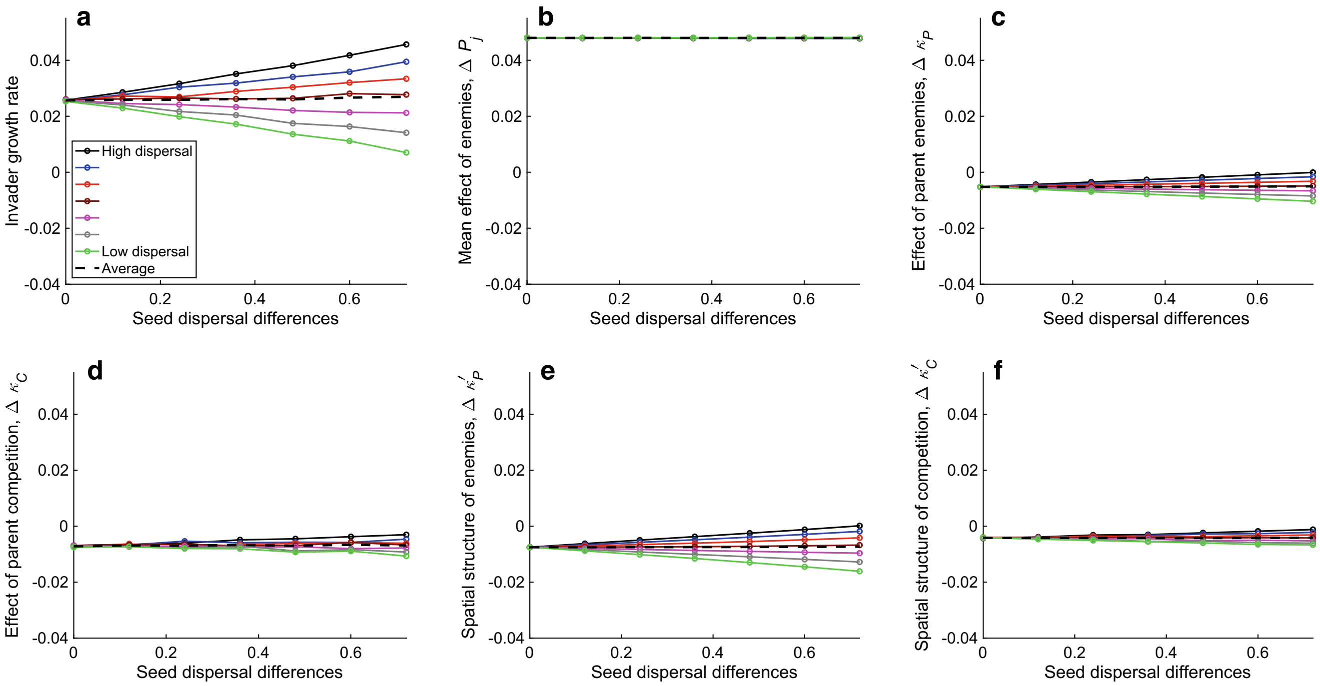

Fig. 4 We simulated an invasion analysis in several communities where species were identical except for their seed dispersal. **a** We show the invader growth rate of each species. Each circle represents a particular species' invader growth rate in a community. Circles at the same x coordinate are coexisting. The lines connecting the circles show the relative level of seed dispersal (i.e., the black line represents the species with the highest dispersal in each community, the middle line represents the species with the fourth highest dispersal). **b–f** We show the Δ mechanisms for each species (excluding ΔY_j, which was the same for all species). In each case, the mechanism makes the most positive (or least negative) contribution to the fitness of the species with the highest dispersal. We used the following parameters: $S = 7$, $p_{\mathrm{A},j} = 0.3$, $p_{\mathrm{S},j} = 0$, $Y_j = 7.8$, $\delta = 0.4$, $l = 10$, $L = 200$. We modeled dispersal as described in Appendix A3; in each community, the α parameter used to model dispersal varied uniformly between species with a mean of 5.1, and a range is given by the x-axis (e.g., a range of 0.36 meant that α varied from 4.92 to 5.28)

We also found that differences in dispersal modify the impact of seedling competition ($\Delta\kappa_{\mathrm{C}j}$ and $\Delta\kappa'_{\mathrm{C}j}$) through an increase in kin-competition (Fig. 4d, f). If a species has low seed dispersal, then sites near an adult of that species tend to have more seeds and therefore higher seedling competition (decreasing $\Delta\kappa_{\mathrm{C}j}$). Additionally, species with low dispersal were more clustered (Fig. 3), further raising seedling competition (decreasing $\Delta\kappa'_{\mathrm{C}j}$). In both cases, these mainly contribute to a mean fitness-difference, rather than a stabilizing mechanism.

Our results show that differences in dispersal mainly create fitness-differences, rather than stabilizing mechanisms (Table 2, Fig. 4a). For example, interspecific differences in dispersal do not change the mean invader growth rates in Fig. 4a, they only change the growth rates of particular species. Species with high dispersal are at an advantage relative to those with low dispersal, and if this advantage outweighs the stabilizing effect of natural enemies, then species with low dispersal species be excluded (Fig. 8g). Dispersal differences alone do not generate stabilizing mechanisms: low-dispersal species do not have a novel niche that reduces competition with high-dispersal species.

Species differ in dispersal and susceptibility to natural enemies

Finally, we consider the case where species can differ in susceptibility to natural enemies (p_j). In this case, the average impact of natural enemies becomes

$$\Delta P_i \approx \frac{\overline{p_j}}{R-1} + \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)],\, p_j\right) - \frac{p_i - \overline{p_j}}{(R-1)^2}, \qquad (16)$$

where $\overline{p_j}$ is the mean of p_j across species, and $\mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)],\, p_j\right)$ is the covariance of $\mathbf{E}[N_j(t)]$ and p_j across species at equilibrium (Appendix A2.2). This approximation of ΔP_i has two novel terms. The last term represents a small fitness effect, which harms species that are more susceptible to natural enemies. The covariance term represents a contribution to the stabilizing effect, as it will be the same across all species. The covariance will be negative, and thus will weaken the stabilizing mechanism, if the species that are most resistant to their natural enemies are most common (because the community will be less regulated by natural enemies overall, (Stump and Comita 2018)). All else being equal, this covariance term will tend to be negative, as natural enemy resistance tends to allow

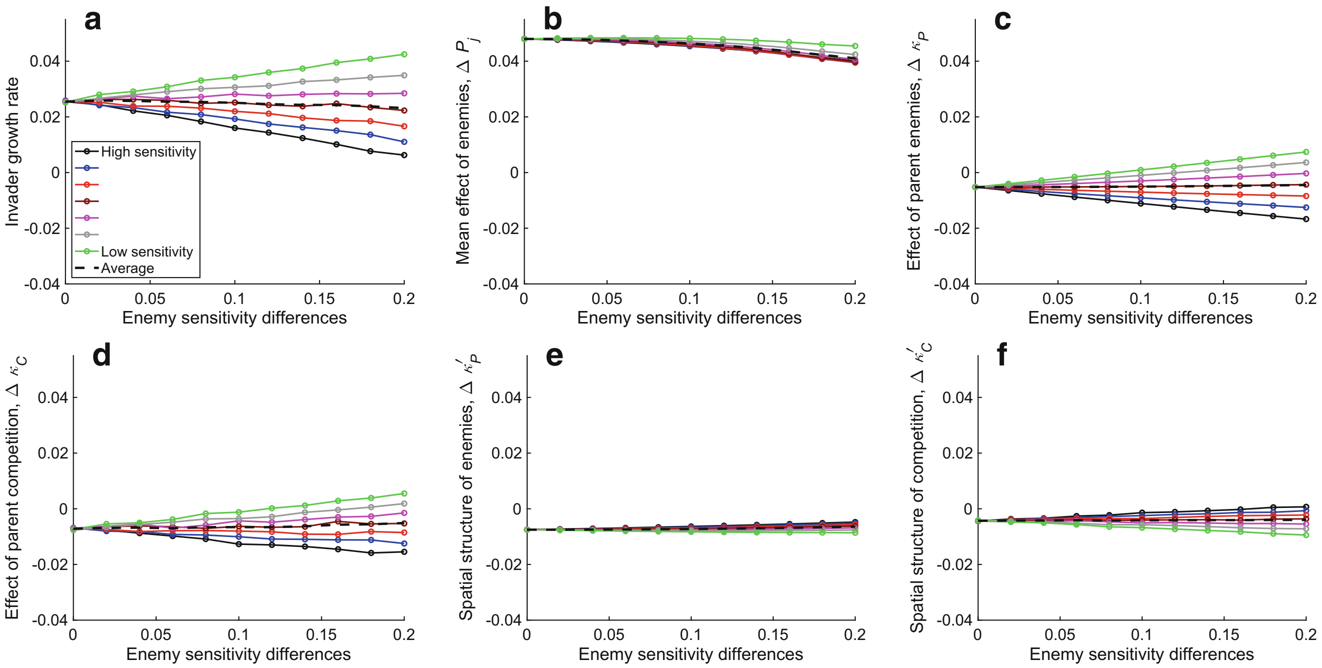

Fig. 5 We simulated an invasion analysis in communities where species were identical except for their sensitivity to natural enemies. **a** We show the invader growth rate of each species. Each circle represents a particular species' invader growth rate in a community. Circles at the same x coordinate are coexisting. **b–f** We show the Δ mechanisms for each species. Most mechanisms are the most positive (or least negative) for the species that is least sensitive to enemies. The two exceptions are $\Delta\kappa_{\mathrm{C}j}$ and $\Delta\kappa'_{\mathrm{C}j}$, because there is more crowding in their sites (i.e., because the seedlings can resist enemies so well). We used the following parameters: $S = 7$, $p_{\mathrm{S},j} = 0$, $Y_j = 7.8$, $\delta = 0.4$, $l = 10$, $L = 200$. We modeled dispersal as described in Appendix A3, and each species had $\alpha_j = 5.1$. $p_{\mathrm{A},j}$ varied uniformly between species with a mean of 0.3

species to become common (Fig. 5a, b). However, we found that a dispersal-susceptibility trade-off can strengthen the stabilizing mechanism: high dispersal increases a species' abundance; thus, a dispersal-susceptibility trade-off can make susceptible species more common and resistant species rarer, making $\mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)],\, p_j\right)$ less negative and boosting the stabilizing mechanism (though this does not always occur, Fig. 6b).

Although a dispersal-susceptibility trade-off may slightly alter the stabilizing mechanism, we find that it often generates a much stronger equalizing effect by reducing the advantage of high dispersal (Fig. 6). Consider the community in Fig. 6: there are large interspecific differences in each of the Δ mechanisms (Fig. 6b–f); however, the invader growth rates (Fig. 6a) remain similar for all species. The chance a seed is killed by its parent's natural enemies is the product of two factors: the chance it encounters those natural enemies ($\widetilde{d_j d_{\mathrm{P},j}}$) and the chance it dies from those natural enemies (p_j). As a result, when p_j can differ between species, $\Delta\kappa_{\mathrm{P}j}$ becomes

$$\Delta\kappa_{\mathrm{P}i} = \approx \frac{-\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}}{R-1} - \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)],\, p_j \widetilde{d_j d_{\mathrm{P},j}}\right) - \frac{R}{R-1}\left(p_i \widetilde{d_i d_{\mathrm{P},i}} - \overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}\right). \tag{17}$$

where $\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}$ is the across-species mean of the product of p_j and $\widetilde{d_j d_{\mathrm{P},j}}$. Note that the third term now depends on the difference in the product of p_j and $\widetilde{d_j d_{\mathrm{P},j}}$, not just $\widetilde{d_j d_{\mathrm{P},j}}$ alone. Thus, a species can have a positive $\Delta\kappa_{\mathrm{P}i}$ if it has high dispersal or low susceptibility. Under a dispersal-susceptibility trade-off, seedlings that are more likely to encounter their parents' natural enemies are less likely to die from them; thus, between-species differences are reduced. Differences in the impact of clumping ($\Delta\kappa'_{\mathrm{P}j}$) are also reduced, as species that are more clustered have seedlings that are more likely to survive in areas with many enemies.

We also tested what happens if dispersal and susceptibility differ randomly between members of the community, rather than according to a trade-off. Here, species with low dispersal and high susceptibility have both disadvantages. However, they could coexist with trees with higher dispersal and lower susceptibility as long as the fitness-differences were smaller than the stabilizing mechanism (Fig. 12b). Interestingly, simulations showed that community assembly itself often produced a trade-off by excluding weaker species (Fig. 12a).

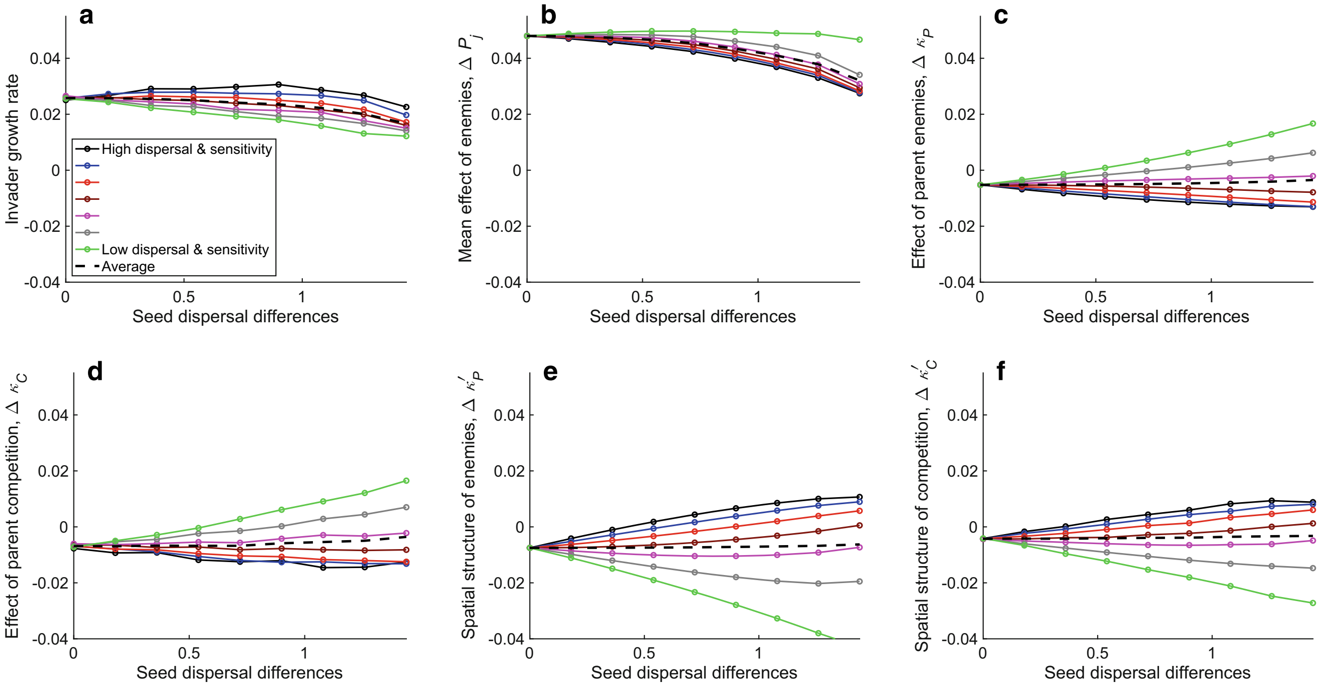

Fig. 6 We simulated an invasion analysis in communities where dispersal traded off with sensitivity to natural enemies. **a** We show the invader growth rate of each species. Each circle represents a particular species' invader growth rate in a community. Circles at the same x coordinate are coexisting. **b**–**f** We show the Δ mechanisms for each species. We used the following parameters: $S = 7$, $p_{\mathrm{S},j} = 0$, $Y_j = 7.8$, $\delta = 0.4$, $l = 10$, $L = 200$. We modeled dispersal as described in Appendix A3. The trade-off was such that the average individual had $\alpha_j = 5.1$ and $p_{\mathrm{A},j} = 0.3$, and increasing $p_{\mathrm{A},j}$ by 0.1 increased α_j by 0.3

Discussion

Specialist natural enemies are thought to be a key driver of tree diversity in tropical forests (Wright 2002; Comita et al. 2014; Terborgh 2015; Levi et al. 2019). However, recent studies have shown that seed dispersal and natural enemy movement alter how natural enemies affect coexistence (Adler and Muller-Landau 2005; Mack and Bever 2014; Stump and Chesson 2015; Miranda et al. 2015; Stump and Comita 2018). Here, we extend this work by using theoretical models to examine how interspecific differences in seed dispersal could modify coexistence. We find that species that disperse their seeds farther are less likely to encounter distance- and density-responsive enemies. On its own, differences in dispersal undermine coexistence by putting low-dispersal species at a disadvantage (Fig. 4). However, empirical ecologists have long suspected that seed dispersal trades off with tolerance to natural enemies (Howe 1993). Such a trade-off can be equalizing, as the species that are most likely to encounter specialist natural enemies are the most resistant to them.

Our results probe the impact that spatial clustering has on coexistence. If a species is spatially aggregated, its seeds are more likely to disperse near conspecifics, and thus more likely to encounter specialist natural enemies. This has two effects. First, we found that spatial structure weakens the stabilizing mechanism by creating a rare species disadvantage: rarer species become more clustered (Fig. 3) and therefore lose more seeds to natural enemies (Fig. 2e). This result agrees with previous theoretical studies suggesting that species will become more aggregated when they become rarer (Usinowicz 2015; Detto and Muller-Landau 2016), as well as empirical evidence that rare tree species tend to be more aggregated than common species (Condit et al. 2000). Second, species that are more clustered are at a competitive disadvantage relative to those that are spread out because seeds are more exposed to natural enemies (Fig. 4d). Our model agrees with previous empirical and theoretical work showing that species with low seed dispersal will be more clustered (Detto and Muller-Landau 2016; Cobo-Quinche et al. 2019). It is also possible that differences in clustering may be caused by habitat preferences, which causes higher survival, and therefore higher densities, at sites with optimal conditions for the species (Plotkin et al. 2002). The interactive effects of seed dispersal, habitat preferences, and specialized enemies should be investigated in future studies to determine their effects on tree species coexistence (though see Stump and Chesson (2015)).

The dispersal-susceptibility trade-off described here differs from previous mechanisms of dispersal-mediated coexistence. For example, the competition-colonization trade-off promotes coexistence if species that quickly colonize empty sites are displaced by stronger competitors that colonize sites more slowly (Hastings 1980; Murrell and Law 2003). Similar mechanisms have been proposed in which species coexist because dispersal trades off with fecundity (Yu and Wilson 2001), survival (Tilman 1994), or the ability to fill in local gaps (Bolker and Pacala 1999). Those models differ from ours because the trade-offs themselves generate a stabilizing mechanism: high-dispersal species have a unique niche because they are more able to compete for empty sites. As a result, a strict trade-off is required; otherwise, species cannot coexist (Hastings 1980; Yu and Wilson 2001). In our model, specialist natural enemies generate the stabilizing mechanism, and the dispersal-susceptibility trade-off modifies their effect. Because of this, a strict trade-off is not required for coexistence (Fig. 12). Rather, the natural enemies set the coexistence bandwidth of the system, and the trade-off helps species remain within that bandwidth. Additionally, in most dispersal trade-off models, coexistence is only possible if there is lots of empty space; otherwise, weak competitors have no competition-free areas to colonize (Hastings 1980; Bolker and Pacala 1999). In our model, high dispersal is advantageous because it helps seeds to escape specialist natural enemies; therefore, it could occur in a crowded community. Dispersal-competition trade-offs have often been criticized for relying on overly stringent and unrealistic assumptions (Levin et al. 2003; Levine and Murrell 2003): high-diversity tropical forests are not known for having empty space, and the diverse morphology of seeds and fruit make a strict dispersal-competition trade-off seem unlikely. As such, we think the dispersal-susceptibility trade-off in this model is more likely to contribute to tropical tree diversity.

Using our methods as a baseline for future simulations

Most previous works on distance-responsive enemies either analyzed simplified models that could not include spatial structure (e.g., (Turnbull et al. 2010; Stump and Chesson 2015; Mack et al. 2019)) or examined spatially explicit models using simulations that did not tease apart the impact of spatial structure from other effects (e.g., (Muller-Landau and Adler 2007; Sedio and Ostling 2013; Mack and Bever 2014; Miranda et al. 2015; Levi et al. 2019)). The hybrid approach here merges these techniques and suggests three effects are critical to understanding how natural enemies affect coexistence (ΔP_j, $\Delta \kappa_{\mathrm{P}j}$, and $\Delta \kappa'_{\mathrm{P}j}$). These factors can easily be measured using simulations, even in models far more complicated than ours.

Our methods suggest a framework for quantifying the impact that natural enemies are having on persistence and coexistence (akin to those in Ellner et al. (2016) and Ellner et al. (2019), who showed generically how to quantify the storage effect using simulations). To use these methods, one would need to perform an invasion analysis and then measure three factors. First, one would calculate the average chance of seed mortality (ΔP_j) by averaging the risk of mortality across the landscape and comparing this effect on invaders vs. residents. ΔP_j quantifies how generally hostile the landscape is to residents and invaders, and if the spatial structure of mortality does not matter, it will be the only non-zero term. Second, one would calculate how much a seed's chance of mortality can be attributed to its parent ($\Delta \kappa_{\mathrm{P}j}$) by randomizing the distribution of adults, calculating a seed's average risk of mortality if it dispersed from a given adult, and subtracting ΔP_j. Third, one would calculate the impact of clustering on mortality ($\Delta \kappa'_{\mathrm{P}j}$) by calculating a seed's average risk of mortality and subtracting $\Delta \kappa_{\mathrm{P}j}$ and ΔP_j. $\Delta \kappa'_{\mathrm{P}j}$ quantifies how the spatial distribution of adults affects mortality rates and coexistence.

Using our model to interpret empirical results

The parameters in our model (Table 1) can be estimated using established techniques. Baseline seedling survival (I_j) can be estimated using long-term seedling plots (see Comita et al. (2010) and Visser et al. (2016)). Seed dispersal kernels ($d_j(z)$) can be estimated by comparing data from seed traps to the spatial distribution of adults (see Clark et al. (1999) and Muller-Landau (2008)). The distribution kernel of distance-responsive enemies ($d_{\mathrm{A},j}(z)$) can be estimated by determining how seedling mortality changes with the distance from conspecific adults (see Augspurger (1983), Becker and Wong (1985), and Comita et al. (2010)). The frequency of adults of each species ($\mathbf{E}[N_j(t)]$) is easily determined from surveys (Hubbell et al. 2005). Seed production (Y_j) can be estimated by comparing the number of seeds found in seed traps to the number of nearby adults, after accounting for dispersal (Muller-Landau 2008; Visser et al. 2016). Adult mortality (δ) can be determined from long-term surveys (Hubbell et al. 2005). The impact of specialist natural enemies (p_j) can be measured by experimentally removing natural enemies (see Fricke et al. (2014) and Krishnadas and Comita (2018)), or conducting a plant-soil feedback experiment (Bever 1994). Alternatively, the impact of natural enemies can be estimated using techniques to measure NDD (see Augspurger and Kelly (1984) and Comita et al. (2010)); however, the latter method comes with the caveats that it cannot distinguish between the impact of natural enemies vs. other sources of NDD (Huntly 1991), estimates may be altered by habitat (Stump and Chesson 2015), and NDD is notoriously hard to measure (Freckleton and Lewis 2006). In either case, p_j

needs to be quantified as the maximum effect that natural enemies could have on survival.

There are three ways our results could be used to study real systems. First, one could parameterize our model and simulate the dynamics of a community. This could be used to test whether species are coexisting, or to examine how a perturbation (e.g., fragmentation) would alter the community; such methods are currently being used in a parallel study (Krishnadas and Stump, *in review*). If the model is accurate and the parameters are correct, then the abundance and spatial structure should match those in the field. This method may be difficult to implement, as it requires knowledge all of the parameters, some of which require a great deal of data to estimate (e.g., seed dispersal kernels). However, one method around this is to use sensitivity tests to determine how critical each parameter is to community dynamics.

Second, one could estimate the stabilizing and fitness effects of the Δ terms using data. The terms that can be estimated are those describing the species' differences in fecundity and survival (ΔY_i), species' differences in the spatially averaged chance of seedling mortality (ΔP_i), species' differences in the chance a seedling will die from its parent's enemy shadow ($\Delta\kappa_{\mathrm{P}j}$), and species' differences in seedling competition in proximity to their parent ($\Delta\kappa_{\mathrm{C}j}$). For example, the stabilizing mechanism produced by the spatial-average impact of natural enemies, ($\overline{\Delta P_j}$), requires estimating the potential NDD ($p_{\mathrm{A},j}$ or $p_{\mathrm{S},j}$) and frequencies of all species ($\mathbf{E}[N_j(t)]$) (Table 2). Estimating the impact of spatial structure on seedling mortality ($\Delta\kappa'_{\mathrm{P}j}$) and seedling competition ($\Delta\kappa'_{\mathrm{C}j}$) is more challenging, as we have no estimates that can be derived purely from model parameters (Table 2). However, we give some suggestions in Appendix A6.1. Measuring the Δ terms will not test if species are coexisting, but rather how much particular factors are helping or reducing species' ability to persist (Barabás et al. 2018).

Third, one could compare Δ terms to describe qualitative impacts on the system. For example, the stabilizing impact of natural enemies is weakened if common species are more tolerant of their natural enemies; this effect is

$$\frac{\overline{\Delta P}\text{with variation in natural enemy susceptibility}}{\overline{\Delta P}\text{without variation in natural enemy susceptibility}} \approx \frac{\left(\frac{\overline{p_j}}{R-1}\right) + \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)],\, p_j\right)}{\left(\frac{\overline{p_j}}{R-1}\right)} \tag{18}$$

(previously shown in Stump and Comita (2018)). Also, low seed dispersal reduces the ability of natural enemies to stabilize coexistence; this effect is

$$\begin{aligned}&\frac{\text{Stabilizing effect with limited dispersal}}{\text{Stabilizing effect with universal dispersal}}\\ &= \frac{\overline{\Delta P} + \overline{\Delta\kappa_{\mathrm{P}}}}{\overline{\Delta P}}\\ &\approx 1 - \overline{\widetilde{d_j d_{\mathrm{P},j}}} - \frac{\mathbf{cov}^{\mathrm{S}}\left(p_j\mathbf{E}[N_j(t)],\, \widetilde{d_j d_{\mathrm{P},j}}\right)}{\left(\frac{\overline{p_j}}{R-1}\right) + \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)],\, p_j\right)}\end{aligned} \tag{19}$$

We explain how to use Eq. 19 in detail in Appendix A6.2, using empirical estimates of seed dispersal for canopy trees on Barro Colorado Island, Panama (Muller-Landau 2008). We roughly estimate that limited seed dispersal reduces the stabilizing effect of density-responsive enemies by about 6%. Finally, one could estimate whether differences in dispersal and susceptibility do produce an equalizing effect; we describe methods for this in Appendix A6.3.

Conclusion

Seed dispersal is the only chance a tree has to move during its lifetime, and it is an important mechanism for escaping specialist natural enemies. However, seed dispersal can vary by an order of magnitude among competitors. Our model suggests that these differences will not stabilize coexistence, though a dispersal-susceptibility trade-off could promote coexistence as an equalizing mechanism. This mechanism does not require a strict trade-off, nor an abundance of empty sites, and thus, we believe it is more likely to be operating in tropical forests. Our results outline quantities that can be measured in simulations and using real-world data and thus lay the groundwork for future studies on the interaction between seed dispersal and distance- and density-responsive enemies.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix A1: Deriving the formula for $\tilde{\lambda}'_j(t)$

A1.1 Size assumptions for analysis

Our analysis is based on Taylor Series approximations. These work well for a parameter range where the populations are approximately quadratic, though may fail if parameters are too extreme. Thus, to bound the amount of variation in our model, we define a "small" parameter ϵ. We write $O(\epsilon)$ to indicate that a parameter is of the same order as ϵ (for a technical definition, see Chesson (1994)). We assume that for all species, $Y_j/Y_k = 1 + O(\epsilon)I_{j/k} = 1 + O(\epsilon)$, p_j is $O(\epsilon)$, and $d_j^2(z)/d_k^2(z) = 1 + O(\epsilon)$, and $(d_{\mathrm{P}-j}(z))^2/(d_{\mathrm{P}-k}(z))^2 = 1 + O(\epsilon)$ for all z. Terms that are smaller than these, such as $(p_j)^2$, are mostly left out of our approximation, leaving the growth rate of species as $\tilde{\lambda}_j'(t) = O(\epsilon)$. We write $\approx$ to indicate that numbers are identical up to their $O(\epsilon)$ terms.

In a few cases in the text, we do not approximate our model as much as we could. For example, in Table 2, we mention that the impact of seedling mortality caused by a seedling's parents, $\Delta\kappa_{\mathrm{P}j}$, contains the term $\left(p_j\widetilde{d_jd_{\mathrm{P},j}} - \overline{p_j\widetilde{d_jd_{\mathrm{P},j}}}\right)$. We could approximate $p_j\widetilde{d_jd_{\mathrm{P},j}}$ using a Taylor series around $p_j = \overline{p_j}$ and $\widetilde{d_jd_{\mathrm{P},j}} = \overline{\widetilde{d_jd_{\mathrm{P},j}}}$ (where $\overline{p_j}$ and $\overline{\widetilde{d_jd_{\mathrm{P},j}}}$ are the means of p_j and $\widetilde{d_jd_{\mathrm{P},j}}$ across species) and get that

$$p_j\widetilde{d_jd_{\mathrm{P},j}} \approx \overline{p_j}\,\overline{\widetilde{d_jd_{\mathrm{P},j}}} + (p_j - \overline{p_j})\overline{\widetilde{d_jd_{\mathrm{P},j}}} + (\widetilde{d_jd_{\mathrm{P},j}} - \overline{\widetilde{d_jd_{\mathrm{P},j}}})\overline{p_j} \tag{20}$$

$\overline{p_j}$ and $(\widetilde{d_jd_{\mathrm{P},j}} - \overline{\widetilde{d_jd_{\mathrm{P},j}}})$ are both $O(\epsilon)$; therefore, the third term is $O(\epsilon^2)$. Thus, we could ignore that term, and our approximation simplifies to $p_j\widetilde{d_jd_{\mathrm{P},j}} \approx p_j\overline{\widetilde{d_jd_{\mathrm{P},j}}}$. However, we found that this leads to poorer approximations. Thus, there were some parts of our analysis where some $O(\epsilon^{1.5})$ and $O(\epsilon^2)$ terms were included implicitly. We feel that the quality of our approximations (Appendix A4) justifies their inclusion and note that previous work has suggested higher order terms will at times be necessary (Chesson 1994; Barabás et al. 2018).

A1.2 Deriving $\tilde{\lambda}_j'(t)$

Equation 1 gives the fitness of an individual of species j. The effect of competition, $C(x, t)$, is the number of seedlings in site x at time t. For a seed that was produced at site y to become a seedling at x, it must disperse there (which it does with probability $d_j(|x-y|)$), and then it must survive its natural enemies. Thus, $C(x, t)$ can be calculated by summing this parameter over all sites and all species. Each adults of species j will disperse $Y_jd_j(|x-y|)$ seeds to x, and therefore, a total of $Y_j\sum_{y=1}^{\infty}N_j(y,t)d_j(|x-y|)$ seeds will be dispersed to x (where the summation is over all sites y). Each of those seeds will then become seedlings with probability $S_j(x, t)$. Thus,

$$C(x,t) = \sum_{j=1}^{R} S_j(x,t)Y_j\sum_{y=1}^{L^2} N_j(y,t)d_j(|x-y|) \tag{21}$$

where $\sum_{j=1}^{R}$ is the summation over all species.

For the text that follows, we write the growth rate as $\lambda_j'(x,t) = (\lambda_j(x,t) - 1)/\delta$, so that fitness is defined as 0 when there is no population growth and it is in per-generation time scale. Thus,

$$\lambda_j'(x,t) = Y_j\sum_{y=1}^{L^2}\frac{d_j(|y-x|)S_j(y,t)}{C(y,t)} - 1. \tag{22}$$

Note that $\lambda_j'(x,t)$ is defined in terms of x (the position of the adult), as it will vary across space (due to the distribution of conspecific and heterospecific adults).

The summation can be seen as a weighted average,

$$\begin{aligned}
&Y_j\sum_{y=1}^{L^2}\frac{d_j(|y-x|)S_j(y,t)}{C(y,t)}\\
&= L^2\mathbf{E}\left[Y_j\frac{d_j(|y-x|)S_j(y,t)}{C(y,t)}\right]\\
&= L^2\mathbf{E}\left[d_j(|y-x|)\right]\mathbf{E}\left[Y_j\frac{S_j(y,t)}{C(y,t)}\right]\\
&+ L^2Y_j\mathbf{cov}\left(d_j(|y-x|), Y_j\frac{S_j(y,t)}{C(y,t)}\right),
\end{aligned} \tag{23}$$

where the covariance is over all sites y. If $S_j(x,t) = I_j(1 + O(\epsilon))$ and $Y_j/Y_k = 1 + O(\epsilon)$ for all j and k (as we assumed), then $\frac{Y_jS_j(y,t)}{C(y,t)} \approx 1 + \ln\left\{Y_j\right\} + \ln\left\{S_j(x,t)\right\} - \ln\left\{C(x,t)\right\}$. Thus,

$$\begin{aligned}
&Y_j\sum_{y=1}^{L^2}\frac{d_j(|y-x|)S_j(y,t)}{C(y,t)} \approx\\
&L^2\mathbf{E}\left[d_j(|y-x|)\right]\left(1 + \ln\left\{Y_j\right\}\right.\\
&+ \left.\mathbf{E}\left[\ln\left\{S_j(y,t)\right\}\right] - \mathbf{E}\left[\ln\left\{C(y,t)\right\}\right]\right)\\
&+ L^2\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\} - \ln\left\{C(y,t)\right\}\right).
\end{aligned} \tag{24}$$

Finally, note that $\sum_{y=1}^{L^2}d_j(|y-x|) = 1$, as it is a dispersal kernel. Thus, $\mathbf{E}\left[d_j(|y-x|)\right] = 1/L^2$, and

$$\begin{aligned}
&Y_j\sum_{y}\frac{d_j(|y-x|)S_j(y,t)}{C(y,t)} \approx\\
&1 + \ln\left\{Y_j\right\} + \mathbf{E}\left[\ln\left\{S_j(y,t)\right\}\right] - \mathbf{E}\left[\ln\left\{C(y,t)\right\}\right]\\
&+ L^2\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right) -\\
&L^2\mathbf{cov}\left(d_j(|y-x|), \ln\left\{C(y,t)\right\}\right).
\end{aligned} \tag{25}$$

Putting these back into Eq. 22,

$$\begin{aligned}
&\lambda_j'(x,t) \approx\\
&\ln\left\{Y_j\right\} + \mathbf{E}\left[\ln\left\{S_j(y,t)\right\}\right] - \mathbf{E}\left[\ln\left\{C(y,t)\right\}\right]\\
&+ L^2\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right)\\
&- L^2\mathbf{cov}\left(d_j(|y-x|), \ln\left\{C(y,t)\right\}\right).
\end{aligned} \tag{26}$$

This equation represents the fitness of an adult at site x. To calculate the finite rate of increase of a population, $\tilde{\lambda}'_j(t)$, we average this over all sites containing adults of species j,

$$\begin{aligned}\tilde{\lambda}'_j(t) &= \mathbf{E}\left[\lambda'_j(x,t)\middle| N_j(x,t)=1\right]\\ &= \mathbf{E}[\lambda'_j(x,t)N_j(x,t)]\left(\mathbf{E}[N_j(t)]\right)^{-1}\\ &= \mathbf{E}\left[\lambda'_j(x,t)\right] + \mathbf{cov}\left(\lambda'_j(y,t), \frac{N_j(y,t)}{\mathbf{E}[N_j(t)]}\right). \qquad (27)\end{aligned}$$

The first term represents the average fitness that an individual would have if it were placed in random location, and the second term describes the impact of spatial structure (Chesson 2000). For example, if species j is rare but highly aggregated, then $\mathbf{E}[\lambda'_j(x,t)]$ will be positive (i.e., the species is rare, so a random adult is unlikely to be in a high-mortality area), but $\mathbf{cov}\left(\lambda'_j(y,t), N_j(y,t)/\mathbf{E}[N_j(t)]\right)$ will be negative (i.e., most of the individuals are aggregated in high-mortality areas). We then substitute Eq. 26 into this. The term $\ln\left\{Y_j\right\}$ and the spatial average terms are already constants, and they will not contribute to the covariance. Thus,

$$\begin{aligned}&\tilde{\lambda}'_j(t) \approx \ln\left\{Y_j\right\} + \mathbf{E}[\ln\left\{S_j(y,t)\right\}] - \mathbf{E}[\ln\left\{C(y,t)\right\}]\\ &+ L^2\mathbf{E}\left[\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right)\right]\\ &- L^2\mathbf{E}\left[\mathbf{cov}\left(d_j(|y-x|), \ln\left\{C(y,t)\right\}\right)\right]\\ &+ L^2\mathbf{cov}\left(\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right), \frac{N_j(x,t)}{\mathbf{E}[N_j(t)]}\right)\\ &- L^2\mathbf{cov}\left(\mathbf{cov}\left(d_j(|y-x|), \ln\left\{C(y,t)\right\}\right), \frac{N_j(x,t)}{\mathbf{E}[N_j(t)]}\right) \quad (28)\end{aligned}$$

(where the outer covariances are over all sites x). This can be simplified further by approximating survival, $S_j(x,t)$. By Eq. 5,

$$\begin{aligned}&\ln\left\{S_j(x,t)\right\} = \ln\left\{I_j\right\} +\\ &\ln\left\{1 - \sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(y,t)\right\}. \qquad (29)\end{aligned}$$

p_j is $O(\epsilon)$; therefore,

$$\ln\left\{S_j(x,t)\right\} \approx \ln\left\{I_j\right\} - \sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(y,t). \qquad (30)$$

The above equation is the reason that our results will hold if $S_j(x,t)$ is an approximately linear function of conspecific density (as stated in the main text); this is why we felt justified modeling $S_j(x,t)$ using a log-likelihood function in our simulations (described below in Appendix A3, Eq. 65). Thus,

$$\begin{aligned}&\tilde{\lambda}'_j(t) \approx \ln\left\{Y_j\right\} - \mathbf{E}\left[\ln\left\{C(y,t)\right\}\right]\\ &+ \ln\left\{I_j\right\} - \mathbf{E}\left[\sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(y,t)\right]\\ &+ L^2\mathbf{E}\left[\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right)\right]\\ &- L^2\mathbf{E}\left[\mathbf{cov}\left(d_j(|y-x), \ln\left\{C(y,t)\right\}\right)\right]\\ &+ L^2\mathbf{cov}\left(\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right), \frac{N_j(x,t)}{\mathbf{E}[N_j(t)]}\right)\\ &- L^2\mathbf{cov}\left(\mathbf{cov}\left(d_j(|y-x|), \ln\left\{C(y,t)\right\}\right), \frac{N_j(x,t)}{\mathbf{E}[N_j(t)]}\right) (31)\end{aligned}$$

A1.3 Invasion analysis and partitioning terms

Here, we perform an invasion analysis. We assume that species i is rare, and the other $R-1$ resident species are at equilibrium in the absence of i. We assume that all species are at a long-term steady state and stable spatial distribution. Because the residents are at equilibrium, $\tilde{\lambda}'_r(t) = 0$ for all $r \neq i$. Thus,

$$\tilde{\lambda}'_i(t) = \tilde{\lambda}'_i(t) - \frac{1}{R-1}\sum_{r\neq i}\tilde{\lambda}'_r(t) \qquad (32)$$

(where the summation is over all resident species). Substituting approximations Eqs. 30 and 31 into the above equation, we can partition the invader growth rate into a series of additive terms.

We combine the terms $\ln\left\{Y_j\right\}$ and $\ln\left\{I_j\right\}$ (giving us $\ln\left\{Y_j I_j\right\}$). Taking the invader-resident difference in this, we are left with ΔY_i in Eq. 7. The invader-resident difference in the fourth term gives us ΔP_i, Eq. 8. The invader-resident difference in the fifth term gives us $\Delta\kappa_{\mathrm{P}i}$, Eq. 10. The invader-resident difference in the sixth term gives $\Delta\kappa_{\mathrm{C}i}$, Eq. 13. The invader-resident difference in the seventh term gives $\Delta\kappa'_{\mathrm{P}i}$, Eq. 13. Finally, the invader-resident difference in the last term gives $\Delta\kappa'_{\mathrm{C}i}$, Eq. 14. Together, this gives us Eq. 6.

Note that Eq. 6 does not have a term comparing the $\mathbf{E}[\ln\left\{C(y,t)\right\}]$ values, as these are the same for all species, and therefore $\mathbf{E}[\ln\left\{C(y,t)\right\}] - \frac{1}{R-1}\sum_{r\neq i}\mathbf{E}[\ln\left\{C(y,t)\right\}] = 0$.

Appendix A2: Simplifying the Δ terms

In this section, we simplify the Δ terms, to give the approximations in Table 2. Additionally, we break them into their stabilizing components (their average over all species), and their mean fitness-difference components (the value for a given species minus the average).

To simplify notation, we define the following:

$$\widetilde{d_j^2} = \mathbf{E}\left[\sum_{y=1}^{L^2}\left(d_j(|x-y|)\right)^2\right]$$

$$\widetilde{d_j d_{\mathrm{P},j}} = \mathbf{E}\left[\sum_{y=1}^{L^2} d_j(|x-y|) d_{\mathrm{p}-j}\left(|x-y|\right)\right]$$

$$\widetilde{d_j d_{\mathrm{P},j}^2} = \mathbf{E}\left[\sum_{y=1}^{L^2} d_j(|x-y|)\left(d_{\mathrm{p}-j}\left(|x-y|\right)\right)^2\right]. \tag{33}$$

Thus, $\widetilde{d_j^2}$ is the sum of $d_j(|x-y|)^2$ over all sites (i.e., the dot product of the dispersal kernel with itself), $\widetilde{d_j d_{\mathrm{P},j}}$ is the sum of the product of $d_j(|x-y|)$ and $d_{\mathrm{p}-j}\left(|x-y|\right)$ over all sites (i.e., the dot product of the dispersal kernel and the enemy distribution kernel), and $\widetilde{d_j d_{\mathrm{P},j}^2}$ is the sum of the product of $d_j(|x-y|)$ and $(d_{\mathrm{p}-j}\left(|x-y|\right))^2$ (i.e., the dot product of the dispersal kernel with the square of the enemy distribution kernel). These terms simplify notation below. For example, we show below that the probability that a seedling is killed by its parent's natural enemies is related to $\widetilde{d_j d_{\mathrm{P},j}}$.

A2.1 Appendix: Simplifying ΔY_j

We first simplify ΔY_i, Eq. 7, which is the invader-resident difference in the term $\ln\left\{Y_j I_j\right\}$. To do this, we rewrite it such that the summation is over all species,

$$\begin{aligned}
\Delta Y_i &= \ln\{Y_i I_i\} - \frac{1}{R-1}\sum_{r\neq i}\ln\{Y_r I_r\} \\
&= \ln\{Y_i I_i\} + \frac{\ln\{Y_i I_i\}}{R-1} \\
&\quad - \frac{\ln\{Y_i I_i\}}{R-1} - \frac{1}{R-1}\sum_{r\neq i}\left(\ln\{Y_r I_r\}\right) \\
&= \frac{(R-1)\left(\ln\{Y_i I_i\}\right) + \left(\ln\{Y_i I_i\}\right)}{R-1} \\
&\quad - \frac{1}{R-1}\sum_{j=1}^{R}\left(\ln\left\{Y_j I_j\right\}\right) \\
&= \frac{R\left(\ln\{Y_i I_i\}\right)}{R-1} - \frac{R}{R-1}\frac{1}{R}\sum_{j=1}^{R}\left(\ln\left\{Y_j I_j\right\}\right) \\
&= \frac{R}{R-1}\left(\ln\{Y_i I_i\} - \overline{\ln\left\{Y_j I_j\right\}}\right).
\end{aligned} \tag{34}$$

When we average ΔY_i over all species, the $\ln\left\{Y_j I_j\right\}$ terms will cancel with $\overline{\ln\left\{Y_j I_j\right\}}$, leaving

$$\overline{\Delta Y} = 0. \tag{35}$$

The fitness effect for species j, $\Delta Y_j - \overline{\Delta Y}$, can thus be written with either Eq. 7 or 34.

A2.2 Simplifying ΔP_j

We next simplify ΔP_i, Eq. 8, which comes from differences in $\mathbf{E}\left[\sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(y,t)\right]$. The only terms that vary spatially are the $N_j(y,t)$ terms. Thus,

$$\begin{aligned}
\Delta P_i &= -\sum_{y=1}^{L^2} p_i d_{\mathrm{p}-i}\left(|y-x|\right)\mathbf{E}\left[N_i(x,t)\right] \\
&\quad + \frac{1}{R-1}\sum_{r\neq i}\sum_{y=1}^{L^2} p_r d_{\mathrm{p}-r}\left(|y-x|\right)\mathbf{E}\left[N_r(x,t)\right] \\
&= -p_i\mathbf{E}\left[N_i(x,t)\right]\sum_{y=1}^{L^2} d_{\mathrm{p}-i}\left(|y-x|\right) \\
&\quad + \frac{1}{R-1}\sum_{r\neq i} p_r\mathbf{E}\left[N_r(x,t)\right]\sum_{y=1}^{L^2} d_{\mathrm{p}-r}(|y-x|).
\end{aligned} \tag{36}$$

$\mathbf{E}\left[N_i(t)\right] = 0$, and $d_j(|y-x|)$ sums to 1, therefore

$$\Delta P_i = \frac{1}{R-1}\sum_{r\neq i} p_r\mathbf{E}\left[N_r(t)\right]. \tag{37}$$

Because $\sum_{r\neq i}\mathbf{E}\left[N_r(t)\right] = 1$, this term is simply $\frac{1}{R-1}$ times the frequency-weighted mean of p_r. This can rewritten as

$$\Delta P_i \approx \frac{1}{(R-1)^2}\sum_{r\neq i} p_r + \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}\left[N_r(t)\right], p_r\right)^{\{-i\}}, \tag{38}$$

where the covariance is over all species except species i. Thus, it tends to be smaller if the most abundant species are the least affected by their natural enemies.

Next, we calculate the stabilizing mechanism. The average of $\frac{1}{R-1}\sum_{r\neq i} p_r$, when averaged over all species, is simply the mean of p_r across species, $\overline{p_j}$. Previous work has suggested that the average of $\mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_r(t)], p_r\right)^{\{-i\}}$ can be approximated as $\mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)], p_j\right)$, calculated over all species when they are at equilibrium (Stump and Comita 2018). Thus,

$$\overline{\Delta P} \approx \frac{\overline{p_j}}{R-1} + \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)], p_j\right). \tag{39}$$

Additionally, previous work has suggested that the difference in the $\mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)], p_j\right)$ terms will have a negligible effect on fitness-differences (Stump and Comita 2018). Thus, the fitness effect of ΔP_j is

$$\begin{aligned}
\Delta P_j - \overline{\Delta P} &\approx \frac{1}{(R-1)^2}\sum_{r\neq i} p_r - \frac{\overline{p_j}}{R-1}\\
&= -\frac{p_i}{(R-1)^2} + \frac{p_i}{(R-1)^2}\\
&+ \frac{1}{(R-1)^2}\sum_{r\neq i} p_r - \frac{\overline{p_j}}{R-1}\\
&= -\frac{p_i}{(R-1)^2} + \frac{1}{(R-1)^2}\sum_{j=1}^{R} p_j - \frac{\overline{p_j}}{R-1}\\
&= -\frac{p_i}{(R-1)^2} + \frac{\overline{p_j}R}{(R-1)^2} - \frac{\overline{p_j}}{R-1}\\
&= -\frac{p_i}{(R-1)^2} + \frac{\overline{p_j}R - \overline{p_j}(R-1)}{(R-1)^2}\\
&= -\frac{p_i - \overline{p_j}}{(R-1)^2}.
\end{aligned} \tag{40}$$

As in previous work (Stump and Comita 2018), this effect is generally minor.

A2.3 Simplifying $\Delta\kappa_{\mathrm{P}j}$

We next simplify $\Delta\kappa_{\mathrm{P}i}$, Eq. 10, which begins as

$$\begin{aligned}
\Delta\kappa_{\mathrm{P}i} &= L^2\mathbf{E}\left[\mathbf{cov}\left(d_i(|y-x|), \ln\{S_i(y,t)\}\right)\right]\\
&- \frac{1}{R-1}\sum_{r\neq i} L^2\mathbf{E}\left[\mathbf{cov}\left(d_r(|y-x|), \ln\{S_r(y,t)\}\right)\right]
\end{aligned} \tag{41}$$

We first calculate the covariance $\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right)$. By the law of total covariance,

$$\begin{aligned}
&\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right) =\\
&\mathbf{E}\left[\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\middle| Z\right)\right]\\
&+ \mathbf{cov}\left(\mathbf{E}\left[d_j(|y-x|)\middle| Z\right], \mathbf{E}\left[\ln\left\{S_j(y,t)\right\}\middle| Z\right]\right),
\end{aligned} \tag{42}$$

where $\mathbf{cov}(X, Y | Z)$ is the covariance of X and Y conditioned on some condition Z (the expectation is then over all possible Z's). We condition our covariances on $|y-x| = z$ (i.e., on the assumption that a seed dispersed a distance z); for notational simplicity, we write this as conditioning on z. The first term is 0, because $d_j(|y-x|)$ will be constant when z is constant. Similarly, $\mathbf{E}\left[d_j(|x-y|)\middle| z\right] = d_j(z)$. Finally, we use our approximation in Eq. 30 to write $\ln\left\{S_j(y,t)\right\}$ as $\ln\left\{Y_j\right\} - \sum_{y=0}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(|y-x|, t)$. The term $\ln\left\{Y_j\right\}$ is constant and thus will not affect the covariance. Thus,

$$\begin{aligned}
&\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right) =\\
-\ &\mathbf{cov}\left(d_j(z), \mathbf{E}\left[\sum_{y=0}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(|y-x|, t)\middle| z\right]\right).
\end{aligned} \tag{43}$$

We next find a formula for the mean impact of natural enemies averaged over space, $\mathbf{E}\left[\sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(y,t)\middle| z\right]$. We are averaging over all possible sites x, so spatial structure does not matter (this is taken into account with $\Delta\kappa'_{\mathrm{P}j}$). Let us define ψ_z as the number of sites a distance z from x. Let us first begin with the z that we are conditioning on, $z = |x-y|$. We know that at least one of those sites must contain a conspecific adult (i.e., the parent of the seed at x). The remaining $\psi_z - 1$ sites will contain a conspecific adult with probability $\mathbf{E}[N_j(t)]$. Thus, there will on average be $\psi_z\mathbf{E}[N_j(t)] + 1 - \mathbf{E}[N_j(t)]$ adults a distance z away (and they will reduce survival by $p_j d_{\mathrm{p}-j}(z)$). At any other distance $w \neq |x-y|$, there will be ψ_w sites, each will contain a conspecific adult with probability $\mathbf{E}[N_j(t)]$, and they will each reduce survival by $p_j d_{\mathrm{p}-j}(w)$. Thus,

$$\begin{aligned}
&\mathbf{E}\left[\sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(y,t)\middle| z\right]\\
&= p_j d_{\mathrm{p}-j}(z)\left(1 - \mathbf{E}[N_j(t)]\right) + \sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}(y-x)\,\mathbf{E}[N_j(t)]\\
&= p_j d_{\mathrm{p}-j}(z)\left(1 - \mathbf{E}[N_j(t)]\right) + p_j\mathbf{E}[N_j(t)]
\end{aligned} \tag{44}$$

Only the first term varies with z. Therefore,

$$\begin{aligned}
&\mathbf{cov}\left(\mathbf{E}\left[d_j(|y-x|)\middle| z\right], \mathbf{E}\left[\ln\left\{S_j(y,t)\right\}\middle| z\right]\right)\\
&= \mathbf{cov}\left(d_j(z), p_j d_{\mathrm{p}-j}(z)\left(1 - \mathbf{E}[N_j(t)]\right) + p_j\mathbf{E}[N_j(t)]\right)\\
&= \left(1 - \mathbf{E}[N_j(t)]\right) p_j\mathbf{cov}\left(d_j(z), d_{\mathrm{p}-j}(z)\right)
\end{aligned} \tag{45}$$

The covariance term $\mathbf{cov}\left(d_j(z), d_{\mathrm{p}-j}(z)\right)$ is $p_j\mathbf{E}[d_j(z)d_{\mathrm{p}-j}(z)] - p_j\mathbf{E}[d_j z]\mathbf{E}[d_{\mathrm{p}-j}(z)]$. The mean of the product is $\frac{1}{L^2}\widetilde{d_j d_{\mathrm{P},j}}$ (by our definition in Eq. 33). The mean of $d_j(z)$ and $d_{\mathrm{p}-j}(z)$ are each L^2, as they are dispersal kernels and therefore must sum to 1 over all L^2 sites. Thus,

$$\begin{aligned}
&\mathbf{E}\left[\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(y,t)\right\}\right)\right]\\
&= \frac{1}{L^2}\left(1 - \mathbf{E}[N_j(t)]\right)\left(p_j\widetilde{d_j d_{\mathrm{P},j}} - \frac{1}{L^2}p_j\right).
\end{aligned} \tag{46}$$

If L is large, we can ignore the $-\frac{1}{L^2}p_j$ term.

Substituting this into Eq. 10

$$\begin{aligned}
\Delta\kappa_{\mathrm{P}i} &\approx -p_i\left(1 - \mathbf{E}\left[N_i(t)\right]\right)\widetilde{d_i d_{\mathrm{P},i}}\\
&\quad + \frac{1}{R-1}\sum_{r\neq i} p_r\left(1 - \mathbf{E}\left[N_r(t)\right]\right)\widetilde{d_r d_{\mathrm{P},r}}\\
&\approx \frac{-1}{R-1}\sum_{r\neq i} p_r\mathbf{E}\left[N_r(t)\right]\widetilde{d_r d_{\mathrm{P},r}}\\
&\quad - \left(p_i\widetilde{d_i d_{\mathrm{P},i}} - \frac{1}{R-1}\sum_{r\neq i} p_r\widetilde{d_r d_{\mathrm{P},r}}\right).
\end{aligned} \tag{47}$$

Using a procedure similar to Eq. 34, this becomes

$$\Delta\kappa_{\mathrm{P}i} \approx \frac{-1}{R-1}\sum_{r\neq i} p_r \mathbf{E}\left[N_r(t)\right] \widetilde{d_r d_{\mathrm{P},r}}$$
$$-\ \frac{R}{R-1}\left(p_i \widetilde{d_i d_{\mathrm{P},i}} - \overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}\right). \tag{48}$$

Thus, averaging across species, this becomes a frequency-weighted mean of $\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}$. We believe that the approximation for $\overline{\Delta P}$ will hold (i.e., that we can approximate the mean of the covariance over invaders as the covariance when all species are at equilibrium); in this case,

$$\overline{\Delta\kappa_{\mathrm{P}}} \approx \frac{\overline{-p_j \widetilde{d_j d_{\mathrm{P},j}}}}{R-1} - \mathbf{cov}^{\mathrm{S}}\left(\mathbf{E}[N_j(t)],\, p_j \widetilde{d_j d_{\mathrm{P},j}}\right). \tag{49}$$

Additionally, if the covariances cancel out of the mean fitness differences, then

$$\Delta\kappa_{\mathrm{P}j} - \overline{\Delta\kappa_{\mathrm{P}}} \approx \left(\frac{-1}{R-1}\sum_{r\neq i} p_r \widetilde{d_r d_{\mathrm{P},r}} \mathbf{E}\left[N_r(t)\right]\right.$$
$$\left. -\frac{R}{R-1}\left(p_j \widetilde{d_j d_{\mathrm{P},j}} - \overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}\right)\right) + \frac{\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}}{R-1}. \tag{50}$$

$\mathbf{E}[N_i(t)] = 0$, and therefore the summation $\sum_{r\neq i} p_r \widetilde{d_r d_{\mathrm{P},r}} \mathbf{E}[N_r(t)]$ over all residents is equal to the summation $\sum_{j=1}^{R} p_j \widetilde{d_j d_{\mathrm{P},j}} \mathbf{E}[N_j(t)]$ over all species. This term is $\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}\ + R\mathbf{cov}^{\mathrm{S}}\left(p_j \widetilde{d_j d_{\mathrm{P},j}}, \mathbf{E}[N_j(t)]\right)$, although if we can cancel out the covariance term, then

$$\Delta\kappa_{\mathrm{P}j} - \overline{\Delta\kappa_{\mathrm{P}}} \approx \left(-\frac{\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}}{R-1} - \frac{R}{R-1}\left(p_j \widetilde{d_j d_{\mathrm{P},j}} - \overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}\right)\right)$$
$$+\ \frac{\overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}}{R-1}$$
$$= -\frac{R}{R-1}\left(p_j \widetilde{d_j d_{\mathrm{P},j}} - \overline{p_j \widetilde{d_j d_{\mathrm{P},j}}}\right). \tag{51}$$

A2.4 Simplifying $\Delta\kappa_{\mathrm{C}j}$

We next simplify $\Delta\kappa_{\mathrm{C}i}$, Eq. 13. Using the law of total covariance and conditioning on $|y-x| = z$ (as before),

$$\mathbf{cov}\left(d_j(|y-x|), \ln\{C(y,t)\}\right) =$$
$$\mathbf{cov}\left(d_j(z), \mathbf{E}\left[\ln\{C(y,t)\}|\, z\right]\right). \tag{52}$$

We next find a formula for $\mathbf{E}\left[\ln\{C(y,t)\}|\, z\right]$. We define $C(j,y,t)$ as the number of seedlings at y of species j; it is

$$C(j,y,t) = \sum_{x=1}^{L^2} d_j(|x-y|) Y_j S_j(y,t) N_j(x,t). \tag{53}$$

Thus, $C(y,t) = \sum_{j=1}^{R} C(j,y,t)$. $C(j,y,t)$ can be rewritten as

$$C(j,y,t) = Y_j\left(I_j\left(1 - p_j\sum_{x=1}^{L^2} d_{\mathrm{p}-j}\left(|x-y|\right) N_j(x,t)\right)\right)\times$$
$$\left(\sum_{x=1}^{L^2} d_j(|x-y|) N_j(x,t)\right). \tag{54}$$

This will be easier to work with if its value is close to $\mathbf{E}[N_j(t)]$. Thus, we next divide this divide both sides by the across-species mean of $Y_j I_j$, which we call $(YI)^*$. Then, we define $\widehat{YI}_j = Y_j I_j/(YI)^* - 1$, and

$$\frac{C(j,y,t)}{(YI)^*} = \left(1+\widehat{YI}_j\right)\left(1 - p_j\sum_{x=1}^{L^2} d_{\mathrm{p}-j}\left(|x-y|\right) N_j(x,t)\right)\times$$
$$\left(\sum_{x=1}^{L^2} d_j(|x-y|) N_j(x,t)\right). \tag{55}$$

We next approximate the conditional average of $C(j,y,t)$ given an $N_j(x,t)$ for some location x. $N_j(x,t)$ it could be 0 or 1, we will define this later. We approximate the mean of $C(j,y,t)$ as the value of $C(j,y,t)$ when $N_j(x,t) = \mathbf{E}[N_j(t)]$; the true mean would include an effect of the variance of $N_j(x,t)$; however, we find that the approximations that this simplification produces fit well (see Appendix A4). Thus,

$$\frac{\mathbf{E}\left[C(j,y,t)|\, N_j(x,t)\right]}{(YI)^*} \approx \left(1+\widehat{YI}_j\right)\times$$
$$\left(1 - p_j\mathbf{E}[N_j(t)] - \left(N_j(x,t) - \mathbf{E}[N_j(t)]\right) p_j d_{\mathrm{p}-j}\left(|x-y|\right)\right)\times$$
$$\left(\mathbf{E}[N_j(t)] + \left(N_j(x,t) - \mathbf{E}[N_j(t)]\right) d_j(|x-y|)\right). \tag{56}$$

Next, we multiply these terms. The term $\widehat{YI}_j$ is $O(\epsilon)$; thus, $\widehat{YI}_j p_j$ will be small, and we will ignore it. If $N_j(x,t) = 0$, this becomes

$$\frac{\mathbf{E}\left[C(j,y,t)|\, N_j(x,t) = 0\right]}{(YI)^*} \approx$$
$$\mathbf{E}[N_j(t)]\left[1 - d_j(|x-y|) + \widehat{YI}_j\left(1 - d_j(|x-y|)\right)\right.$$
$$\left. -p_j\mathbf{E}[N_j(t)]\left(1 + d_{\mathrm{p}-j}\left(|x-y|\right)\right)\left(1 - d_j(|x-y|)\right)\right]. \tag{57}$$

If $N_j(x,t) = 1$,

$$\frac{\mathbf{E}\left[C(j,y,t)|\, N_j(x,t) = 1\right]}{(YI)^*} \approx$$
$$\frac{\mathbf{E}\left[C(j,y,t)|\, N_j(x,t) = 0\right]}{(YI)^*} + d_j(|x-y|)$$
$$+\ \widehat{YI}_j d_j(|x-y|) - p_j d_j(|x-y|) d_{\mathrm{p}-j}\left(|x-y|\right)$$
$$-\ p_j d_j(|x-y|)\mathbf{E}[N_j(t)]\left(1 - d_{\mathrm{p}-j}\left(|x-y|\right)\right)$$
$$-\ p_j d_{\mathrm{p}-j}\left(|x-y|\right)\mathbf{E}[N_j(t)]\left(1 - d_j(|x-y|)\right). \tag{58}$$

For notational simplicity, we will define $\xi_j(|x-y|,t)$ as the amount that a seed of species j would change seedling competition at y by being at x,

$$\begin{aligned}\xi_j(|x-y|,t) &= \frac{\mathbf{E}\left[C(j,y,t)|\,N_j(x,t)=1\right]}{(YI)^*}\\ &- \frac{\mathbf{E}\left[C(j,y,t)|\,N_j(x,t)=0\right]}{(YI)^*}\\ &\approx -p_j\left(d_j(|x-y|)d_{\mathrm{p}-j}\left(|x-y|\right)\right.\\ &- 2\mathbf{E}[N_j(t)]d_j(|x-y|)d_{\mathrm{p}-j}\left(|x-y|\right)\\ &\left.+\mathbf{E}[N_j(t)]d_j(|x-y|)+\mathbf{E}[N_j(t)]d_{\mathrm{p}-j}\left(|x-y|\right)\right)\\ &+ d_j(|x-y|)+\widehat{YI}_j d_j(|x-y|).\end{aligned} \tag{59}$$

We can write the mean of $C(y,t)$ using the $C(j,y,t)$ terms

$$\frac{\mathbf{E}\left[C(y,t)\right]}{(YI)^*} = \sum_{j=1}^{R}\frac{\mathbf{E}\left[C(k,y,t)\right]}{(YI)^*} \tag{60}$$

(summed over all species k). If we focus on a particular site x, then this could also be written as

$$\begin{aligned}\frac{\mathbf{E}C(y,t)}{(YI)^*} &= \sum_{k=1}^{R}\frac{\mathbf{E}\left[C(k,y,t)|\,N_k(x,t)=0\right]}{(YI)^*}\\ &+\sum_{k=1}^{R}\mathbf{E}\left[N_k(t)\right]\xi_j(|x-y|,t),\end{aligned} \tag{61}$$

i.e., the first term is the impact of all sites other than x, and the second term is the specific contribution that site x has on seedling competition at y. If we knew that species j occupied x, then

$$\begin{aligned}\frac{\mathbf{E}\left[C(y,t)|\,N_j(x,t)=1\right]}{(YI)^*} &= \sum_{k=1}^{R}\frac{\mathbf{E}\left[C(k,y,t)|\,N_j(x,t)=0\right]}{(YI)^*}\\ &+ \xi_j(|x-y|,t).\end{aligned} \tag{62}$$

Thus, combining the above two equations,

$$\begin{aligned}\frac{\mathbf{E}\left[C(y,t)|\,N_j(x,t)=1\right]}{(YI)^*} &= \frac{\mathbf{E}[C(y,t)]}{(YI)^*}+\xi_j(|x-y|,t)\\ &-\sum_{k=1}^{R}\mathbf{E}[N_k(t)]\xi_j(|x-y|,t).\end{aligned} \tag{63}$$

The terms $\mathbf{E}[C(y,t)]$ and $(YI)^*$ are within $O(\epsilon)$, and thus their ratio will be close to 1. Additionally, the $\xi_j(|x-y|,t)$ terms be within $O(\epsilon)$. Thus, if we take the natural log of both sides and cancel the $\ln\{(YI)^*\}$ terms, then we are left with

$$\begin{aligned}\ln\left\{\mathbf{E}\left[C(y,t)|\,N_j(x,t)=1\right]\right\} &\approx \ln\{\mathbf{E}[C(y,t)]\}\\ &+\xi_j(|x-y|,t)-\sum_{j=1}^{R}\mathbf{E}[N_j(t)]\xi_j(|x-y|,t).\end{aligned} \tag{64}$$

Plugging (64) into our formula for the covariance, Eq. 52

$$\begin{aligned}&\mathbf{cov}\left(d_j(|y-x|),\ln\{C(y,t)\}\right)\approx\\ &\mathbf{cov}\left(d_j(z),\xi_j(d,t)-\sum_{k=1}^{R}\mathbf{E}[N_j(t)]\xi_k(d,t)\right).\end{aligned} \tag{65}$$

(Note that the $\ln\{\mathbf{E}[C(y,t)\}]$ terms cancel, as they are constant). Therefore,

$$\begin{aligned}\Delta\kappa_{\mathrm{C}i} &\approx -\mathbf{cov}\left(d_i(z),\xi_i(z,t)-\sum_{j=1}^{R}\mathbf{E}[N_j(t)]\xi_j(z,t)\right)\\ &+\frac{1}{R-1}\sum_{r\neq i}\mathbf{cov}\left(d_r(z),\xi_r(z,t)-\sum_{j=1}^{R}\mathbf{E}[N_j(t)]\xi_j(z,t)\right).\end{aligned} \tag{66}$$

Our attempts at simplifying this equation further resulted in a poor approximation. Thus, we leave it as this. The stabilizing effect is thus the above equation averaged over species, and the fitness effect is the above equation minus the across-species average.

A2.5 Simplifying the $\Delta\kappa'$ terms

The terms $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$ account for the effects of spatial aggregation. In order to find a simple approximation, we would need an approximation for the spatial structure of each species. We were unable to derive this from first principals. Thus, we need to study its behavior using computer simulations. Here, we outline how these terms can be calculated from simulations.

We begin with $\Delta\kappa'_{\mathrm{P}j}$. The average probability that a seed would survive can be determined by calculating the mean survival of seeds produced by each adult, and is

$$\frac{1}{Y\mathbf{E}[N_j(t)]L^2}\sum_{x=1}^{L^2}Y_jN_j(x,t)\sum_{y=1}^{L^2}d_j(|y-x|)S_j(y,t). \tag{67}$$

Thus, the per-seed average of $\ln\left\{S_j(y,t)\right\}$ can be simplified to

$$\begin{aligned}&\left(\text{per-seed mean}\ln\left\{S_j(y,t)\right\}\right)\\ &= \frac{1}{Y\mathbf{E}[N_j(t)]L^2}\sum_{x=1}^{L^2}Y_jN_j(x,t)\sum_{y=1}^{L^2}d_j(|y-x|)\ln\left\{S_j(y,t)\right\}\\ &= \mathbf{E}[\ln\left\{S_j(y,t)\right\}]+\mathbf{cov}\left(d_j(|y-x|),\ln\left\{S_j(y,t)\right\}\right)\\ &+ \mathbf{cov}\left(d_j(|y-x|)\ln\left\{S_j(y,t)\right\},N_j(x,t)\right).\end{aligned} \tag{68}$$

Thus,

$$\begin{aligned}&\mathbf{cov}\left(d_j(|y-x|)\ln\left\{S_j(y,t)\right\},N_j(x,t)\right)\\ &= \left(\text{per-seed mean}\ln\left\{S_j(y,t)\right\}\right)\\ &- \mathbf{E}[\ln\left\{S_j(y,t)\right\}]-\mathbf{cov}\left(d_j(|y-x|),\ln\left\{S_j(y,t)\right\}\right)\end{aligned} \tag{69}$$

The effect of I_j will cancel out of the mean log seed survival and $\mathbf{E}[\ln\{S_j(y,t)\}]$. Putting this into our resident-invader comparison, we find that

$$\begin{aligned}\Delta\kappa'_{\mathrm{P}i} \approx{} & \Big[(\text{per-seed mean } \ln\{S_i(y,t)\}) \\ & - \frac{1}{R-1}\sum_{r\neq i}(\text{per-seed mean } \ln\{S_r(x,t)\})\Big] \\ & - \Delta P_i - \Delta\kappa_{\mathrm{P}i}. \end{aligned} \tag{70}$$

This result is somewhat tautological—we wanted to quantify the species-specific differences in the per-seed average log chance of seed survival, so we defined the third term as the per-seed average log chance minus the other two terms. We did this because it was mathematically correct (by definition), and because each term represents a qualitatively different effect. And, intuitively, the covariance in $\Delta\kappa'_{\mathrm{P}j}$ is any impact on the per-seed mean log survival that could not be explained by the other two effects. This equation would be useless if ΔP_i and $\Delta\kappa_{\mathrm{P}i}$ could not be independently verified; however, as we show in the next section, we were able to run simulations where spatial aggregation was removed (i.e., so that $\Delta\kappa'_{\mathrm{P}j}$ would be 0 on average). We found that, indeed, the community dynamics could be predicted fairly accurately by ΔP_j, $\Delta\kappa_{\mathrm{P}j}$, $\Delta\kappa_{\mathrm{C}j}$, and ΔY_j.

We can show similarly that the per-seed mean of $\ln\{C(y,t)\}$ (i.e., the average amount of competition experienced by a species) is

$$\begin{aligned} & (\text{per-seed mean} \ln\{C(y,t)\})_j \\ & = \frac{1}{Y\mathbf{E}[N_j(t)]L^2}\sum_{x=1}^{L^2} Y_j N_j(x,t)\sum_{y=1}^{L^2} d_j(|y-x|)\ln\{C(y,t)\} \\ & = \mathbf{E}[\ln\{C(y,t)\}] + \mathbf{cov}\left(d_j(|y-x|), \ln\{C(y,t)\}\right) \\ & + \mathbf{cov}\left(d_j(|y-x|)\ln\{C(y,t)\}, N_j(x,t)\right). \end{aligned} \tag{71}$$

Therefore,

$$\begin{aligned}\Delta\kappa'_{\mathrm{C}i} \approx{} & \Big((\text{per-seed mean} \ln\{C(y,t)\})_i \\ & - \frac{1}{R-1}\sum_{r\neq i}(\text{per-seed mean} \ln\{C(x,t)\})_r\Big) - \Delta\kappa_{\mathrm{C}i}. \end{aligned} \tag{72}$$

In Appendix A3, we run several simulations and check how $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$ vary with a species mean dispersal distance and resident-invader state.

Appendix A3: Computer simulations

In this section, we describe how we implemented our computer simulations.

To speed computation, our model worked with the Manhattan distance function (i.e., the distance between (x_1, y_1) and (x_2, y_2) is $|x_1 - x_2| + |y_1 - y_2|$), rather than the Euclidean distance function (i.e., the distance between (x_1, y_1) and (x_2, y_2) is $\sqrt{(x_1-x_2)^2 + (y_1-y_2)^2}$). The area of a circle is different under each distance function, which affects how many trees are a given distance away. For example, imagine we placed point in a grid, with each point separated by 1 m; then, say we selected a focal point. Under the Manhattan distance function, there would be 20 points a distance 5 m away from the focal point; however, under the Euclidean distance function, there would be 28 points between 4.5 and 5.5 m away from the focal point. But, given that none of our analysis depends on the distance function used (and indeed, $d_{\mathrm{A},j}(z)$ and $d_j(z)$ are arbitrary), we do not believe that this qualitatively affected our results.

We model dispersal using a discrete approximation of a 2-dimensional t (2Dt) distribution. The probability distribution function of a 2Dt distribution with mean 0 and 2 degrees of freedom (i.e., the pdf that a seed will disperse a distance z if it is equally likely to disperse in every direction) is

$$D(z) = \frac{2\pi z}{\pi\exp\{\alpha_j\}(1 + z^2\exp\{-\alpha_j\})^2} \tag{73}$$

where α_j is a species-specific parameter. Note that the $2\pi z$ in the numerator is used because $D(z)$ calculates the chance that it lands in anywhere a distance z away; this is generally left off to model the chance that it lands at a particular location a distance $D(z)$ away. As stated above, Euclidean and Manhattan distances are different; thus, when we were generating seed dispersal kernels, we decided to preserve the probability that a seed would disperse a given distance, rather than the probability it would disperse to a given point.

In our simulations, we calculate $d_j(z)$ as follows: A seed that does not disperse beyond $l/2$ (i.e., half a site) remains in its parent's site, and a seed that disperses between $l(z-0.5)$ and $l(z+0.5)$ is dispersed to one of the $4z$ sites a distance z away with equal likelihood. To reduce computational load, we assume that if a seed dispersed more than $5.5l$, then it was placed in a random site (this could include sites within 5 sites, though the impact was trivial if L was large). Thus,

$$d_j(z) = \begin{cases} \int_0^{l/2} D(y)dy + \int_{5.5l}^{\infty}\frac{D(y)}{L^2}dy & z = 0 \\ \frac{1}{4z}\int_{l(z-0.5)}^{l(z+0.5)} D(y)dy + \int_{5.5l}^{\infty}\frac{D(y)}{L^2}dy & 1 \leq z \leq 5 \\ \int_{5.5l}^{\infty}\frac{D(y)}{L^2}dy & z > 5 \end{cases} \tag{74}$$

We modeled the community as a torus (i.e., a seed that moved off one side was warped to the other side), so that there were no edge effects.

In simulation, we modeled survival such that enemies affected tho log-odds probability of survival, rather than having a linear impact on survival. We did this so that survival would never become negative, and because this connected better with empirical literature (Comita et al. 2010). However, when $p_{\mathrm{A},j}$ and $p_{\mathrm{S},j}$ were small, the log-odds function is close enough to linear to be approximated by Eq. 2. We defined the terms $\tilde{I}_j$ and $\tilde{p}_j$, such that survival on the log-odds scale was

$$S_j(x,t) = \text{logit}\left(\tilde{I}_j - \sum_{y=1}^{L^2} \tilde{p}_j d_{\text{p}-j}\left(|x-y|\right) N_j(y,t)\right). \tag{75}$$

To relate these terms to our previous definitions, $\tilde{I}_j$ was defined as the inverse logit of I_j (i.e., so that when there are no natural enemies, survival is I_j) and $\tilde{p}_j$ was defined as $p_j(1+\exp\{\tilde{I}_j\})$ (i.e., so that a small increase ϵ in the number of nearby conspecifics reduces survival by approximately $p_j\epsilon$).

We modeled the impact of distance-responsive enemies as declining exponentially according an exponential distance function (Comita et al. 2010). We calculate survival at the midpoint of a site (which was 0.25 sites for the parent's site) and ignore adults more than 5 sites away. Thus,

$$d_{\text{A},j}(z) = \begin{cases} c_1 \exp\{-0.25c_2\} & z = 0 \\ c_1 \exp\{-c_2 z\} & 1 \le z \le 5 \\ 0 & z > 5 \end{cases} \tag{76}$$

where c_1 is a distance constant and c_2 is a constant that allows $d_{\text{A},j}(z)$ to sum to 1. In all cases below, we chose $c_2 = 0.5$ (to match empirical literature of 0.2 per m, Comita et al. (2010)), and $c_1 = 0.752$.

A3.1 Computational details for running simulations

We modeled sites as $l\;$ =10 m squares, and usually simulated a 200 × 200 site (400 ha) community. The simulation was usually initiated by filling each site with a random individual with equal likelihood. In cases where one species' density was held constant, we randomly filled that number of sites with the focal species and filled the remainder by randomly selecting the $R-1$ other species with equal probability.

Each time step, we examined each adult to determine if it died. If it survived, then there was no change; if the adult died, then we calculated the number of seeds that were expected to fall in each site. Thus, an individual of species j at site x would contribute $Y_j d_j(|y-x|)$ seeds to site y. We then calculated the impact of distance- and density-responsive enemies. If there were $s_j(y)$ seeds of species j at y, then every seed's log-odds survival was reduced by $s_j(y)\tilde{p}_j^{\text{S}}$; similarly, an adult of species j at x reduced the log-odds survival to species j seedlings at y by $\tilde{p}_j^{\text{A}} d_j^{\text{A}}(|y-x|)$. We used these to calculate $S_j(y,t)$ and used this to calculate the expected number of seedlings at each site (it was rarely a whole number). We then chose a species randomly in proportion to the relative fraction of seedlings at the site. This procedure was repeated each time step.

In some cases, we held the frequency of one species constant. To do this, we began each time step by recording where each individual of that species was located. We then calculated the births and deaths across the community as described above. At the end of the time step, we calculated the amount that the focal population changed in order to estimate $\tilde{\lambda}'_j(t)$, and the values needed to estimate our Δ terms. If the population had increased by n individuals, then we randomly killed n individuals of the focal population. If the population had decreased by n, then we randomly selected n individuals that had died (i.e., using the record from the start of the time step) and restored them.

We performed invasion analyses using the following steps. First, we simulated a community for 2000 time steps, to eliminate any species that was not coexisting. We also recorded the mean frequency of each remaining species. Then, each species was selected in turn to be an invader. We removed the invader and increased every other species' density proportionately. We then simulated the community dynamics for 100 time steps, so that it could reach equilibrium and a stable spatial structure. We then introduced a small number of invader individuals (typically 50 adults). The invaders were placed in random locations, replacing the adult that was there. We ran community dynamics for several time steps (typically 13 time steps, or 5 generations), so that the invader could build up a spatial distribution, but not so long that they became common. We then continued to run the simulation for 37 time steps, and each time step, recorded data on the invader. We calculated the expected value of $\tilde{\lambda}'_j(t)$ by calculating the probability that species j captures each site (i.e., the number of seedlings divided by the total number of seedlings, both after accounting for natural enemies), dividing that value by $\mathbf{E}[N_j(t)]$, multiplying that value by δ, and adding $(1-\delta)$. We also calculated ΔY_j, ΔP_j, $\Delta\kappa_{\text{P}j}$, $\Delta\kappa_{\text{C}j}$, $\Delta\kappa'_{\text{P}j}$, and $\Delta\kappa'_{\text{C}j}$, using approximations derived in Appendix A2. We averaged our results over 37 time steps and ran 120 replicate simulations. It was rare for an invader to die off stochastically, but when it did, we only recorded growth and the Δ values when it was alive.

A3.2 Parameter sets

The six parameter sets used for figures are listed in Table 3. In all cases, we assumed that $\tilde{I}_j = -1$ for all species (i.e., $I_j \approx 0.27$), that, $\delta = 0.4$, and that $\tilde{p}_{\text{A},j} = \tilde{p}_{\text{S},j}$. We generated parameters for 8 species, though in some cases not all persisted. The "trade-off" parameter set assumed that there was a strict trade-off between α_j and $\tilde{p}_j$, such that increasing $\tilde{p}_j$ by 0.1 increased α_j by 0.5. The "equal sensitivity" parameter set assumed that α_j varied, but all species had the same $\tilde{p}_j$ value; this was used to isolate the particular effects of differences in dispersal. Similarly, the "equal dispersal" parameter set assumed that $\tilde{p}_j$ varied, but

α_j was the same between species and was used to isolate the impact of differences in natural enemy susceptibility. In the "yield differences" parameter set, species differ in only their yield values; we also assumed that $\tilde{p}_j$ values were higher than in other parameter sets. We also included two "random parameters" sets, in which $\tilde{p}_j$, α_j, and Y_j were selected randomly (without replacement) from the same distribution; these were used to test what would occur if there was not a strict trade-off.

We tested several additional parameter sets during our analysis. We included a community where species differed in $\tilde{p}_j$ and had near-universal dispersal, we tested two parameter sets that lacked specialist natural enemies, and we tested an additional random parameter set. We chose not to include these data, because we felt they did not add anything. We also ran similar parameter sets but changed the range over which α_j and $\tilde{p}_j$ could vary, and parameters where $\tilde{p}_{\mathrm{A},j} \neq \tilde{p}^{\mathrm{S}}_j$ (including $\tilde{p}^{\mathrm{S}}_j = 0$). Our results were basically similar.

Appendix A4: Checking our approximation

In this section, we describe how we used our computer simulations to check our analytical approximations. We simulated a community without spatial structure. We did this by randomly rearranging the community at the end of each time step (a method previously referred to as the "shaken" method, (Stump et al. 2018b)). This allowed us to remove the effects of spatial structure generated by clumped adult distributions (i.e., the $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$ terms), without removing the impact than adult had on its offspring (i.e., the $\Delta\kappa_{\mathrm{P}j}$ and $\Delta\kappa_{\mathrm{C}j}$ terms).

We studied our model in two ways. First, we performed invasion analysis on our model. We calculated the $\Delta\kappa'_{\mathrm{P}i}$ and $\Delta\kappa'_{\mathrm{C}i}$ values for each invader i, and averaged them over the 120 simulations. The approximations for $\Delta\kappa'_{\mathrm{P}i}$ and $\Delta\kappa'_{\mathrm{C}i}$ calculates the actual impact of natural enemies and competition, and then subtract out the expectation in a model without adult spatial structure. Thus, if our approximation of the non-spatial structure case is accurate, then we predict that $\Delta\kappa'_{\mathrm{P}i}$ and $\Delta\kappa'_{\mathrm{C}i}$ should be approximately 0 on average.

Second, we attempted to study our model in a non-invasion context. We could no longer assume that $\tilde{\lambda}'_j(t) = 0$ for all species; however, because the community had a fixed number of sites, $\mathbf{E}[N_j(t)]\tilde{\lambda}_j$ needed to sum to 1 across all species. Thus, for all species

$$\tilde{\lambda}'_j(t) = \tilde{\lambda}'_j(t) - \sum_{r=1}^{R} \mathbf{E}\left[N_r(t)\right] \tilde{\lambda}'_r(t) \tag{77}$$

where the summation is over all species. We then defined the following terms:

$$\begin{aligned}
\widetilde{\Delta Y_j} &= \ln\left\{Y_j\right\} + \ln\left\{I_j\right\} - \sum_{r=1}^{R} \mathbf{E}\left[N_r(t)\right] \left(\ln\left\{Y_r\right\} + \ln\left\{I_r\right\}\right). \\
\widetilde{\Delta P_j} &= -\mathbf{E}\left[\sum_{y=1}^{L^2} p_j d_{\mathrm{p}-j}\left(|y-x|\right) N_j(|y-x|, t)]\right] \\
&\quad + \sum_{r=1}^{R} \mathbf{E}\left[N_r(t)\right] \mathbf{E}\left[\sum_{y=1}^{L^2} p_r d_{\mathrm{p}-r}\left(|y-x|\right) N_r(|y-x|, t)\right] \\
\widetilde{\Delta\kappa_{\mathrm{P}j}} &= -L^2 \mathbf{E}\left[\mathbf{cov}\left(d_j(|y-x|), \ln\left\{S_j(x,t)\right\}\right)\right] \\
&\quad + \sum_{r=1}^{R} \mathbf{E}\left[N_r(t)\right] L^2 \mathbf{E}\left[\mathbf{cov}\left(d_r(|y-x|), \ln\left\{S_j(x,t)\right\}\right)\right] \\
\widetilde{\Delta\kappa_{\mathrm{C}j}} &\approx -L^2 \mathbf{E}[\mathbf{cov}\left(d_j(|y-x|), \ln\left\{C(y,t)\right\}\right)] \\
&\quad + \sum_{r=1}^{R} \mathbf{E}\left[N_r(t)\right] L^2 \mathbf{E}[\mathbf{cov}\left(d_r(|y-x|), \ln\left\{C(y,t)\right\}\right)]
\end{aligned} \tag{78}$$

Therefore, if spatial structure in the adult community had no effect,

$$\tilde{\lambda}'_j(t) \approx \widetilde{\Delta Y_j} + \widetilde{\Delta P_j} + \widetilde{\Delta\kappa_{\mathrm{P}j}} + \widetilde{\Delta\kappa_{\mathrm{C}j}}. \tag{79}$$

To test the quality of our approximation, we simulated a shaken community with a large number of sites. We compared this to a community which was governed by the above dynamical system. All of the parameters and initial conditions were identical; thus, if our approximation perfectly represented the simulation, their dynamics would be identical to within demographic stochasticity. Additionally, at each time step, we calculated the covariance between seed density at a site x and both $\ln\left\{S_j(x,t)\right\}$ and $\ln\{C(x,t)\}$, along with our estimates for the covariance between those terms at $d_j(|y-x|)$, Eqs. 46 and 65.

Our approximations performed extremely well. Our approximation tended to slightly overestimate the invader growth rate of each species (Fig. 7). The measured values of $\Delta\kappa'_{\mathrm{P}i}$ and $\Delta\kappa'_{\mathrm{C}i}$ tended to be close to 0. For example, in the six communities in Fig. 7, $\overline{\Delta\kappa'_{\mathrm{P}}}$ was measured to be between -0.0016 and -0.0033, and $\overline{\Delta\kappa'_{\mathrm{C}}}$ was between -0.0020 and -0.0036 (i.e., indicating that there was this much error). In the non-equilibrium setting, our predictions from Eqs. 78 and 79 tended to match the simulations fairly well (Fig. 8). Additionally, during the simulations, the measured the covariance between seeds at x and both $\ln\left\{S_j(x,t)\right\}$ and $\ln\{C(x,t)\}$ closely matched our estimates for those terms (Fig. 8).

Appendix A5: Studying our model with simulations

In this section, we describe how we used computer simulations to analyze our model.

Table 3 Parameters in displayed figures. If only one number is given, then all species have that value for that parameter

Name	Parameters								
Trade-off	$\tilde{p}_{\mathrm{A},j} =$	(0.15,	0.193,	0.235,	0.279,	0.321,	0.365,	0.407,	0.45)
	$\alpha_j =$	(4.5,	4.71,	4.93,	5.14,	5.36,	5.57,	5.79,	6)
	$Y_j =$	7.8							
Equal sensitivity	$\tilde{p}_{\mathrm{A},j} =$	0.3							
	$\alpha_j =$	(4.5,	4.71,	4.93,	5.14,	5.36,	5.57,	5.79,	6)
	$Y_j =$	7.8							
Equal dispersal	$\tilde{p}_{\mathrm{A},j} =$	(0.15,	0.193,	0.235,	0.279,	0.321,	0.365,	0.407,	0.45)
	$\alpha_j =$	5.25							
	$Y_j =$	7.8							
Yield differences	$\tilde{p}_{\mathrm{A},j} =$	0.3							
	$\alpha_j =$	5.25							
	$Y_j =$	(7.5,	7.59,	7.67,	7.76,	7.84,	7.79,	8.01,	8.1)
Random parameters	$\tilde{p}_{\mathrm{A},j} =$	(0.231,	0.45,	0.407,	0.236,	0.279,	0.193,	0.364,	0.15)
	$\alpha_j =$	(4.71,	5.57,	5.14,	6,	4.93,	4.5,	5.36,	5.79)
	$Y_j =$	(7.5,	7.59,	7.67,	7.76,	7.84,	7.79,	8.01,	8.1)
Random parameters 2	$\tilde{p}_{\mathrm{A},j} =$	(0.364,	0.407,	0.193,	0.45,	0.321,	0.15,	0.236,	0.279)
	$\alpha_j =$	(5.57,	5.78,	4.71,	6,	5.36,	4.93,	5.14,	4.5)
	$Y_j =$	(7.5,	7.59,	7.67,	7.76,	7.84,	7.79,	8.01,	8.1)

First, simulations suggest that spatial structure made communities less stable (similar results have been shown by Bolker and Pacala (1999) and Durrett and Levin (1994)). In several of our parameter sets, fewer species persisted when there was spatial structure than when there was no spatial structure. For example, in the "equal sensitivity" parameter set, 8 species persisted without spatial structure, but only 6 persisted with spatial structure. In the "equal dispersal" parameter set, 8 species persisted without spatial structure, but only 7 persisted with spatial structure. In the "Random

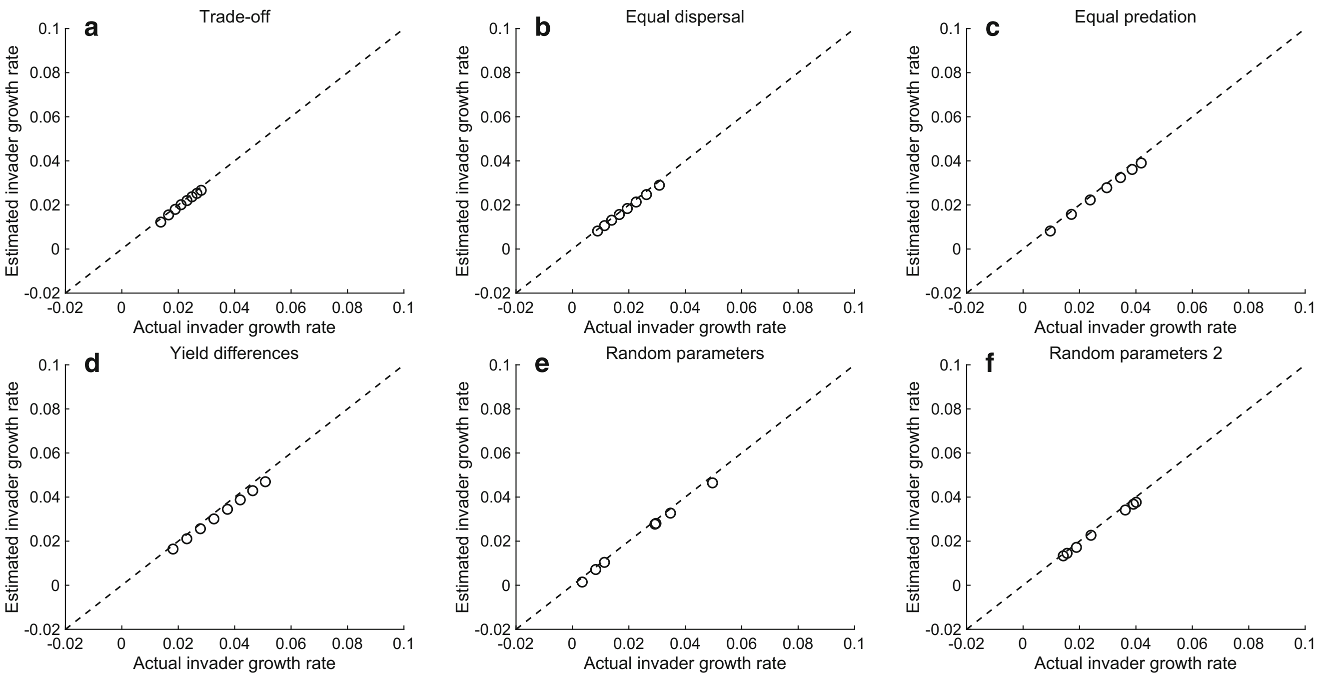

Fig. 7 We ran invasion analyses on communities without spatial structure (i.e., using the shaken model) and compared its outcome to invasion analyses run using using Eqs. 78 and 79. Each dot represents the invader growth rate of a particular species. If the approximations were perfect, the dots would be on the one-to-one line. Each graph lists the parameter set used in the title

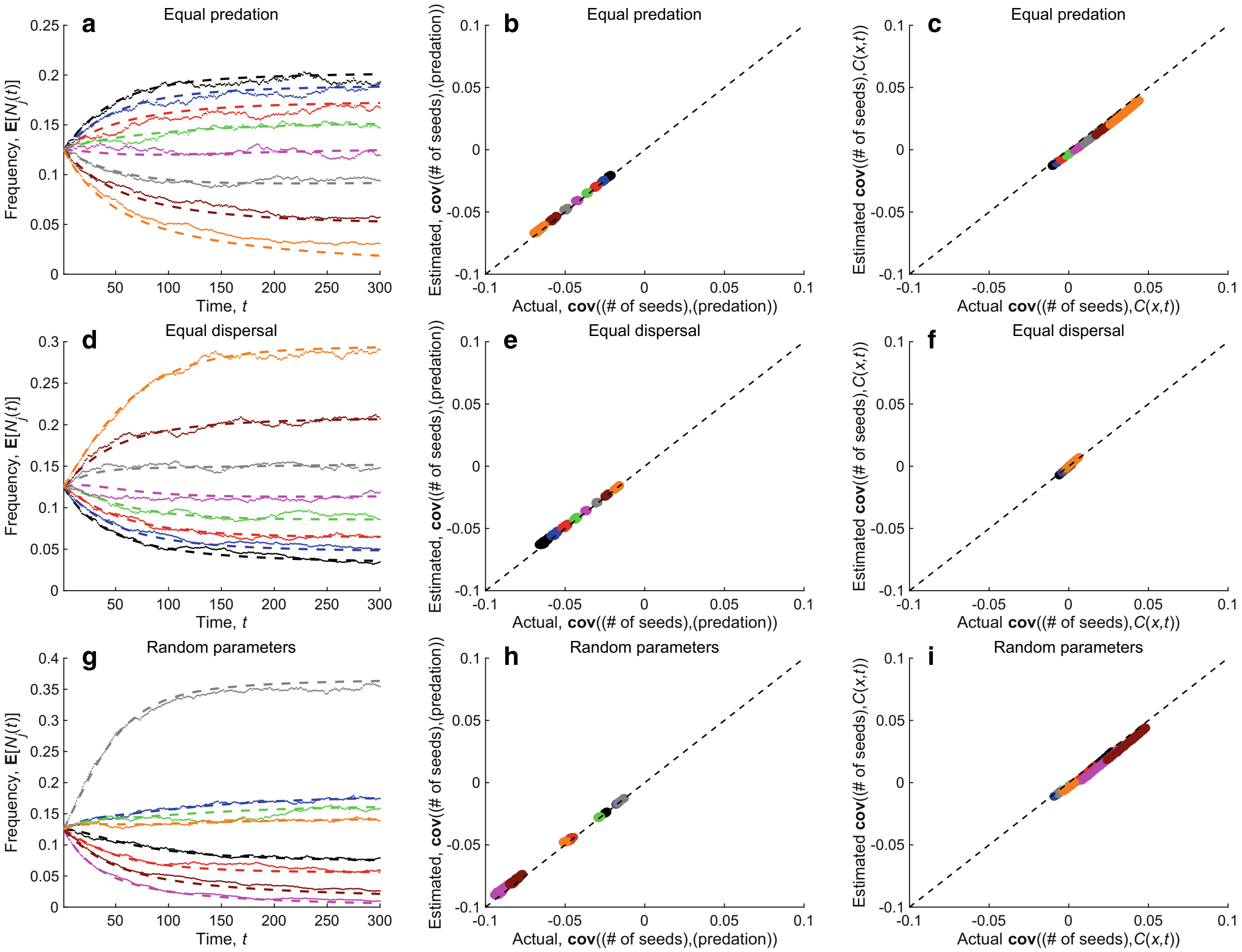

Fig. 8 **a** We simulated a community without spatial structure (i.e., using the shaken model) in a large community ($L = 300$) and present the populations as the solid lines. We also simulated the growth of the community using Eqs. 78 and 79 and present the populations as the dotted lines (corresponding colors were the same species). We used “equal sensitivity” parameters. **b** At each time step of the simulation, we recorded $\mathbf{cov}\left(\text{seed density at } x, \sum_{y=1}^{L^2} p_i d_{\mathrm{p}-j}\left(|y-x|\right) N_j\left(|y-x|, t\right)\right)$, and also used Eq. 46 to estimate what it should be. Each dot represents an estimate at one time point for one species (different colors refer to different species). If our approximation was exact, all dots would be exactly over the one-to-one line. **c** This graph is similar to **b**, except comparing $\mathbf{cov}\left(\text{seed density at } x, \ln\left\{C(x,t)\right\}\right)$ to approximation (65). **d** through **f** are the same as **a** through **c**, except with the “equal dispersal” parameters. **g** through **i** are the same as **a** through **c**, except with the “random” parameters

parameter” set, 7 species persisted without spatial structure, and 5 persisted without spatial structure. Additionally, when we ran an invasion analysis on a community with spatial structure, and then compared this to an identical community without spatial structure (i.e., a shaken model), we found that invader growth rates were lower with spatial structure (Fig. 9). In general, differences in invader growth rates can mostly be attributed to the impacts of spatial structure, $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$. For example, in the communities shown in Fig. 9, the $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$ terms explained between 67% and 98% of the difference between the simulated community and the non-spatial approximation. The remaining differences are likely caused in part by demographic stochasticity in simulations, but could also be caused by shifts in the relative abundances (which would impact $\overline{\Delta P_j}$).

The impact of adult aggregation on mortality risk, $\Delta\kappa'_{\mathrm{P}j}$, appeared to undermine diversity. In all of the our parameter sets, $\overline{\Delta\kappa'_{\mathrm{P}j}}$ was negative (i.e. it was destabilizing). It was always lower than $\overline{\Delta\kappa_{\mathrm{P}j}}$, and often about twice the magnitude. $\Delta\kappa'_{\mathrm{P}j}$ also produced fitness differences, which tended to be smaller in magnitude than the fitness differences produced by $\Delta\kappa_{\mathrm{P}j}$. We also found that $\Delta\kappa'_{\mathrm{P}j}$ was negative for all species in nearly every simulation we ran,

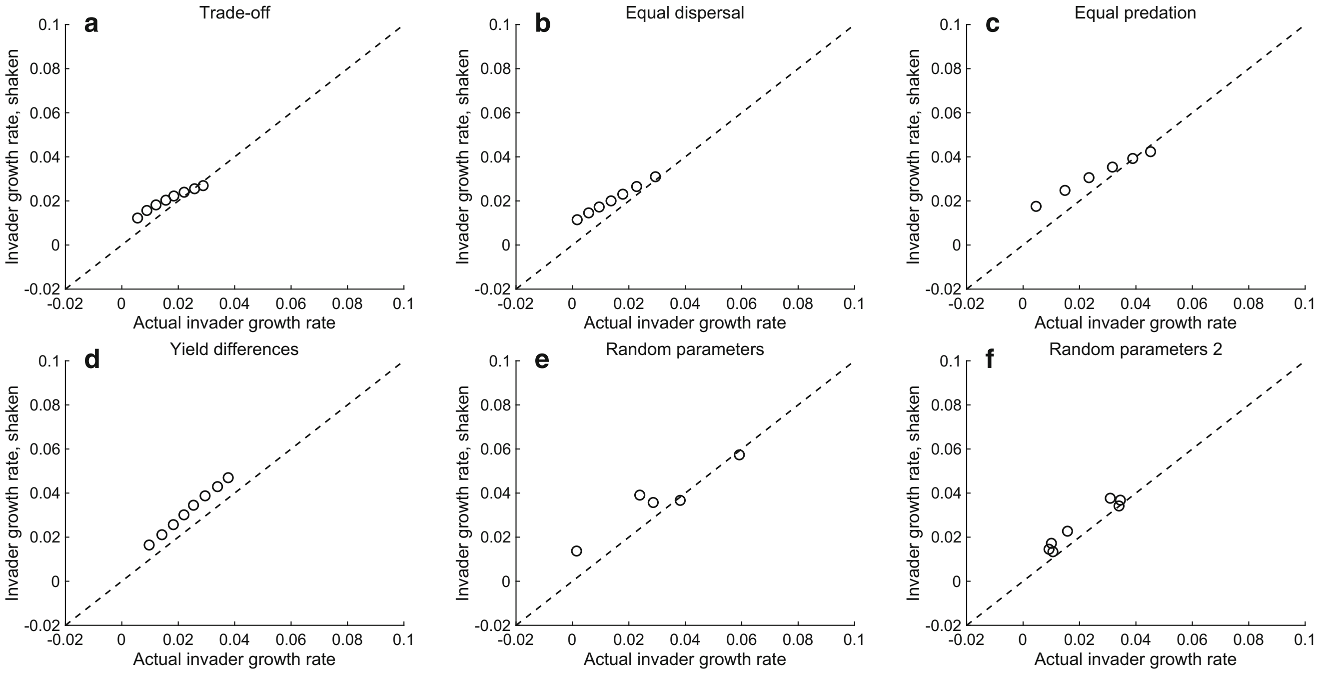

Fig. 9 We ran invasion analyses on communities with spatial structure, and compared its outcome to invasion analyses run using Eqs. 78 and 79 (which does not account for spatial structure). Each dot represents the invader growth rate of a particular species. If a dot is below the line, it indicates that spatial structure reduced that species' invader growth rates. Each graph lists the parameter set used in the title

i.e. that even the biggest fitness advantage granted by $\Delta\kappa'_{\mathrm{P}j}$ could not make up for its destabilizing effect.

The impact of adult aggregation on competition, $\Delta\kappa'_{\mathrm{C}j}$, also undermined diversity, though the impact was less strong. In all cases, $\overline{\Delta\kappa'_{\mathrm{C}j}}$ was negative; however, its actual effect was typically small, and usually much smaller than $\overline{\Delta\kappa_{\mathrm{C}j}}$ and $\overline{\Delta\kappa'_{\mathrm{P}j}}$. It also tended to produce fitness effects; the fitness effects were always smaller than those of $\Delta\kappa_{\mathrm{C}j}$ (the impact of the parent on competition), but could be bigger than the fitness effects of natural enemies.

We found a strong and consistent correlation between a species' abundance and its aggregation. Measuring aggregation as $\ln\{g(3)-1\}$ (i.e. the natural log of the pair correlation at 3 sites, or 30m, minus 1), we found that across our parameter sets, frequency and aggregation was approximately

$$\ln\{g(3)-1\} \approx a + b\mathbf{E}[N_j(t)] \tag{80}$$

for some a and b. In most cases, the slope of the line for a particular species was about -1.2. This varied slightly but was always between -1.1 and -1.25 in the parameter range we tested. We are not sure why this occurred, and how much it was driven by our specific parameters. The intercept value, a differed between species. It appeared that dispersal differences had the biggest impact on a, with species with high dispersal being the least aggregated. Additionally, species with strong potential NDD had a lower a, i.e. were less aggregated, though the impact was slightly weaker than the impact of dispersal.

We found that the terms the covariance between seed density and both $\ln\left\{S_j(x,t)\right\}$ and $\ln\{C(x,t)\}$, the covariance which contribute to $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$, tend to increase with pair correlation function. For example, in Figs. 10 and 11 we show how they change with the pair correlation at 30m for the three different datasets. The $\ln\left\{S_j(x,t)\right\}$ covariance increases with clustering in all cases, and the $\ln\{C(x,t)\}$ covariance increases with clustering in all but 1 case. Both of these covariances contribute negatively to population growth, thus, the fact that they increase shows why $\overline{\Delta\kappa'_{\mathrm{P}}}$ and $\overline{\Delta\kappa'_{\mathrm{C}}}$ both destabilize coexistence.

The covariance terms $\mathbf{cov}\left(\text{seed density at } x, \ln\left\{S_j(x,t)\right\}\right)$ and $\mathbf{cov}\,(\text{seed density at } x, \ln\{C(x,t)\})$ differ significantly between species, even if they are at the same clustering (Figs. 10 and 11). This shows how $\overline{\Delta\kappa'_{\mathrm{P}}}$ and $\overline{\Delta\kappa'_{\mathrm{C}}}$ produce fitness differences. The differences occur because the covariances are driven by other factors as well. For example, species that are more susceptible to natural enemies will have a stronger value of $\mathbf{cov}\left(\text{seed density at } x, \ln\left\{S_j(x,t)\right\}\right)$. Similarly, species with low seed dispersal will have a higher value of the covariance $\mathbf{cov}\left(\text{seed density at } x, \ln\left\{S_j(x,t)\right\}\right)$, because their seeds are more likely to stay in high-mortality areas.

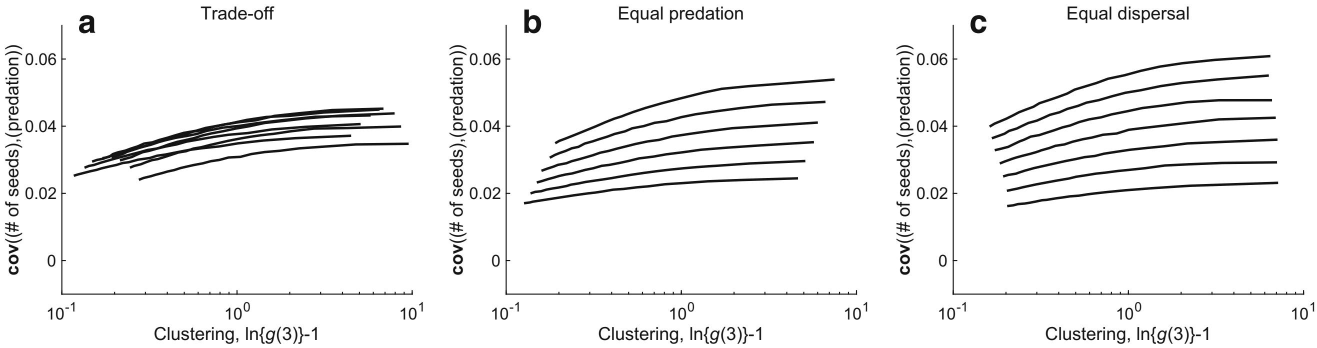

Fig. 10 We simulated community dynamics, holding one species' abundance constant. We tracked how clustered the adult population was at each abundance, and also what $\mathbf{cov}\left(\text{seed density at } x,\ \sum_{y=1}^{L^2} p_i d_{\text{p}-i}\left(|y-x|\right) N_i\left(|y-x|, t\right)\right)$ was at that abundance. Each line represents a different species

Finally, we tested if trade-offs would emerge naturally due to community assembly. To do this, we randomly assembled communities of 15 species. Each species was given a potential NDD for distance-responsive enemies $(p_{\text{A},j})$ and a dispersal distance parameter (α_j); these values were assigned randomly without replacement. Additionally, potential NDD for distance-responsive enemies, $p_{\text{S},j}$, was assigned as $0.78 p_{\text{A},j}$. We calculated the correlation between $p_{\text{A},j}$ and α_j among the 15 species. We then simulated community dynamics for 1500 time steps, to determine which species persisted. We then calculated the correlation between $p_{\text{A},j}$ and α_j among species that persisted. We repeated this for 150 communities.

Community assembly tended to create a positive correlation between p_j^{A} and α_j, such that species that dispersed farther were more susceptible to enemies (Fig. 12a). Our initial communities began with 0 correlation on average, though this varied with a standard deviation of 0.26. On average, 9.3 species survived in a given random community. The average correlation between $p_{\text{A},j}$ and α_j among survivors was 0.43 (with a standard deviation of 0.29), it was positive in 92% of simulations, and was higher than the initial community in 97% of simulations.

Additionally, these results show that while a trade-off would help species coexist, a strict trade-off was not necessary, as it is for the competition-colonization trade-off and many other models of dispersal-mediated coexistence. In fact, a strict trade-off did not emerge in any of our 150 communities. Fig. 12b shows an example of this. Here, 9 of the original 15 species persisted. Among survivors, the species with the third highest dispersal has the third lowest enemy susceptibility, making that species strictly better than 5 of its 8 competitors. However, filtering still produced a correlation of 0.39; this occurred because the species that were susceptible to natural enemies could not survive unless they had reasonably high dispersal, and species that had low dispersal could not survive unless they were tolerant of their natural enemies.

Appendix A6: Measuring terms empirically

In this section, we discuss how various model parameters could be measured empirically.

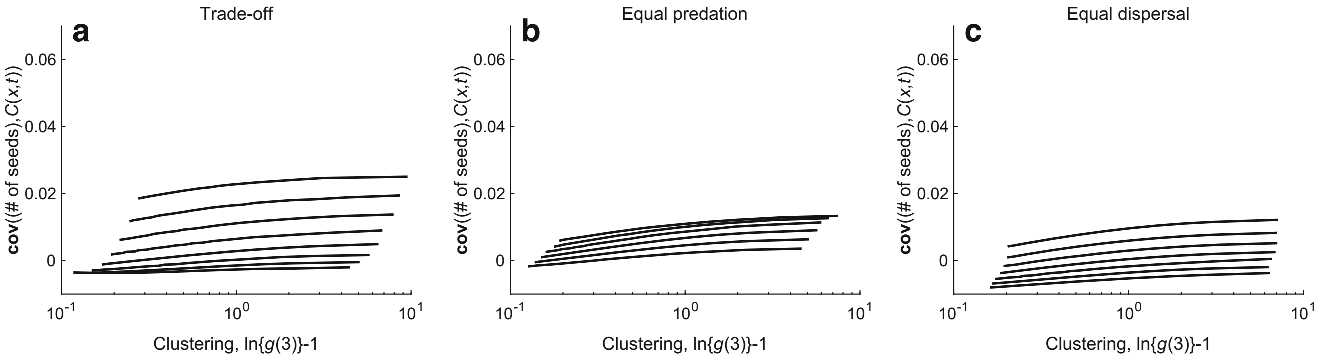

Fig. 11 We simulated community dynamics, holding one species' abundance constant. We tracked how clustered the adult population was at each abundance, and also what $\mathbf{cov}\left(\text{seed density at } x, \ln\left\{C(x,t)\right\}\right)$ was at that abundance. Each line represents a different species

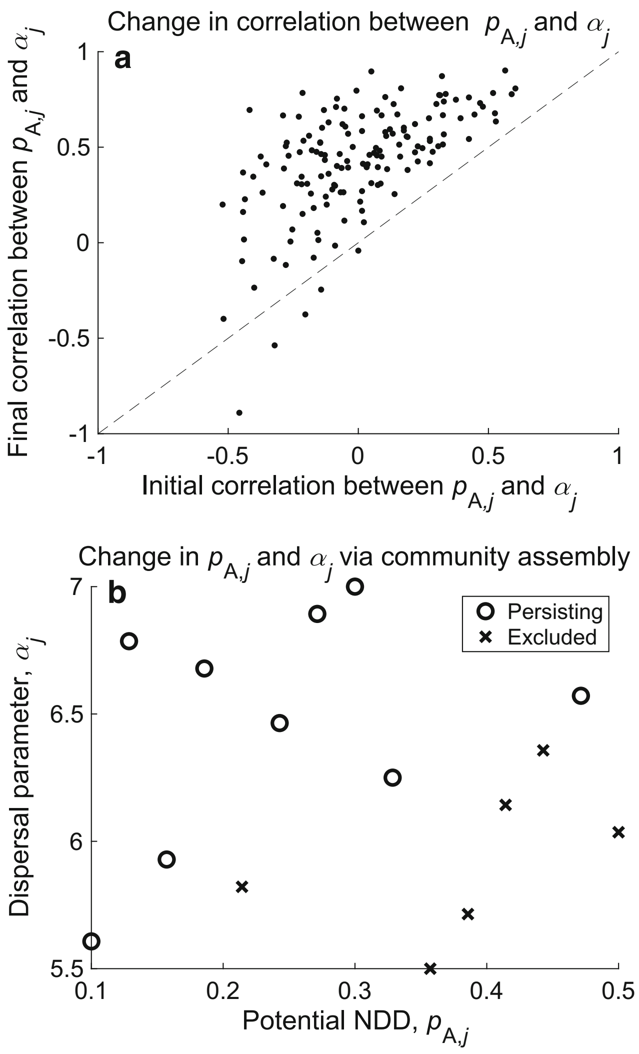

Fig. 12 **a** We assembled communities out of 15 species. Each individual had its $p_{\mathrm{A},j}$ and α_j values assigned randomly from a distribution (without replacement). We then allowed the species to compete, and determine which persisted. We calculated the correlation between $p_{\mathrm{A},j}$ and α_j for all 15 species, and for those that persisted; each dot represents one such comparison. A positive correlation indicates that species that dispersed farther were more sensitive to their natural enemies (i.e. a trade-off was was occurring). $p_{\mathrm{A},j}$ values were uniformly distributed from 0.1 to 0.5. α_j values were uniformly distributed from 5.5 to 7. $p_{\mathrm{S},j}$ values were set to $0.78 p_{\mathrm{A},j}$. For other parameters, we used: $I_j = 0.27$, $\delta = 0.4$, $L = 120$, $l = 10$, and $Y_j = 7.8$. **b** Here we show one such randomly assembled community. Each circle represents a species that persisted, and each x represents a species that was excluded. In the initial community, the correlation between $p_{\mathrm{A},j}$ and α_j was −0.04; in the final community, the correlation was 0.39

A6.1 Measuring $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$

The terms $\Delta\kappa'_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j}$ quantify how the spatial distribution of adults affects the amount of seedling mortality (due to natural enemies) and seedling competition that species experience. We believe that elements of them can be measured in an equilibrium setting. To do this, one would need to map the distribution of seedlings in many locations and estimate the impact of natural enemies at each location. This was done, for example, by Comita et al. (2010), who tracked seedling survival across 20,000 plots in Barro Colorado Island, Panama. Alternatively, one could grow seedlings in soil collected from many locations (using standard methods for plant-soil feedback studies; (Mangan et al. 2010)). First, the covariance that would produce $\Delta\kappa'_{\mathrm{P}j} + \Delta\kappa_{\mathrm{P}j}$ can be quantified as the covariance between seedling density and seedling mortality. For species j, one would need to calculate the expected chance that a seedling of species j would die in each of the 20,000 plots, and calculate how this covaries with the actual number of seedlings in each plot, and then divide this by the mean number of seedlings found per plot. It is unclear what would be the best way to estimate survival in a plot without seedlings (such sites could be left out, or perhaps estimated using a regression model). Similarly, the covariance that would produce $\Delta\kappa'_{\mathrm{C}j} + \Delta\kappa_{\mathrm{C}j}$ is the covariance between the number of species j seedlings in a plot and the total number of seedlings in that plot, divided by the mean number of species j seedlings in a plot.

The above method has a few drawbacks. First, both of these effects calculate the total impact of spatial structure (i.e. including the impact of the seedling's parent); this is probably preferable, though if the impact of the parent needs to be removed, one could subtract what we expect $\Delta\kappa_{\mathrm{P}j}$ and $\Delta\kappa_{\mathrm{C}j}$ to be (based on our model). Second, the method for calculating $\Delta\kappa'_{\mathrm{P}j} + \Delta\kappa_{\mathrm{P}j}$ technically measures the spatial structure of seedling survival, rather enemies specifically. It could potentially be flawed if habitat partitioning is occurring, and species are clustered in areas where they have high density-independent survival (Stump and Chesson 2015). Similarly, the method for calculating $\Delta\kappa'_{\mathrm{C}j} + \Delta\kappa_{\mathrm{C}j}$ is based on the assumption that inter- and intraspecific competition are similar (i.e. that crowding matters, but not which species are causing the crowding); our method will give an inaccurate picture if this assumption is far from true. Last, both measure the covariances in an equilibrium condition, whereas $\Delta\kappa'_{\mathrm{P}j} + \Delta\kappa_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j} + \Delta\kappa_{\mathrm{C}j}$ are for invasion situations. This could still be useful, as it would likely indicate the scope of fitness differences. It could also be used to test some of our models predictions, such as that the covariances contributing to $\Delta\kappa'_{\mathrm{P}j} + \Delta\kappa_{\mathrm{P}j}$ and $\Delta\kappa'_{\mathrm{C}j} + \Delta\kappa_{\mathrm{C}j}$ will be higher for species with low seed dispersal, and for rarer species.

A6.2 Measuring how limited seed dispersal reduces the stabilizing mechanism

In this section, we derive (19) of the main text, which shows how limited seed dispersal reduces the stabilizing effect of natural enemies. We then give an example of how one could measure this, using parameter estimates from Muller-Landau et al. (2008).

The basic principal of Eq. 19 is that we calculate what the stabilizing effect from $\overline{\Delta P_j}$ and $\overline{\Delta\kappa_{\mathrm{P}j}}$ are, and divided this by what it would be if seeds had 100% dispersal (i.e. $\overline{\Delta P_j}$ alone). The term $\overline{\Delta P_j}$ is the mean of $p_j\mathbf{E}[N_j(t)]$, and $\overline{\Delta\kappa_{\mathrm{P}j}}$ is the mean of $-p_j\widetilde{d_j d_{\mathrm{P},j}}\mathbf{E}[N_j(t)]$. Thus,

$$\begin{aligned}\frac{\overline{\Delta P_j}+\overline{\Delta\kappa_{\mathrm{P}j}}}{\overline{\Delta P_j}} &\approx \frac{\overline{p_j\mathbf{E}[N_j(t)]}-\overline{p_j\widetilde{d_j d_{\mathrm{P},j}}\mathbf{E}[N_j(t)]}}{\overline{p_j\mathbf{E}[N_j(t)]}}\\ &= 1-\frac{\overline{p_j\mathbf{E}[N_j(t)]}\,\overline{\widetilde{d_j d_{\mathrm{P},j}}}+\mathbf{cov}\left(p_j\mathbf{E}[N_j(t)],\widetilde{d_j d_{\mathrm{P},j}}\right)}{\overline{p_j\mathbf{E}[N_j(t)]}}\\ &= 1-\overline{\widetilde{d_j d_{\mathrm{P},j}}}-\frac{\mathbf{cov}\left(p_j\mathbf{E}[N_j(t)],\widetilde{d_j d_{\mathrm{P},j}}\right)}{\overline{p_j\mathbf{E}[N_j(t)]}} \qquad (81)\end{aligned}$$

$\widetilde{d_j d_{\mathrm{P},j}}$ is the chance a seed encounters its parent's natural enemies, and the second term is the mean of that term across species. Of course, this effect is not the same for all species, and the third term accounts for this variation. That third term is not the same as $\frac{1}{R-1}\mathbf{cov}\left(p_j,\widetilde{d_j d_{\mathrm{P},j}}\right)+\overline{p_j}\mathbf{cov}\left(\mathbf{E}[N_j(t)],\widetilde{d_j d_{\mathrm{P},j}}\right)$, though it is a good enough approximation for intuition. First, if there is a dispersal-sensitivity trade-off, then the species with the highest p_j (those most susceptible to natural enemies) will have the lowest $\widetilde{d_j d_{\mathrm{P},j}}$ (i.e. most seeds will escape their parents natural enemies); in this case, the covariance will be negative, and thus the stabilizing mechanism will be strengthened. However, if the species that are the most common have the highest dispersal (which we might expect given the fitness advantage), then this will contribute positively to the covariance, and therefore reduce the stabilizing mechanism.

The third term requires significantly more information to assess. As such, simply quantifying $\overline{\widetilde{d_j d_{\mathrm{P},j}}}$ will give a first rough estimate, as it will show how much limited seed dispersal weakens the mechanism in the absence of a dispersal-sensitivity trade-off. If a dispersal-sensitivity trade-off is occurring, then $\overline{\widetilde{d_j d_{\mathrm{P},j}}}$ is an upper-bound of how harmful limited seed dispersal is.

To give an example of how this can be done, we used data from Muller-Landau et al. (2008). They estimated dispersal kernels for 41 species on Barro Colorado Island, Panama. For our work, we focused on the 26 canopy tree species they used ("canopy species" defined in (Comita et al. 2007)). Those values are in Table 4. In a few cases, Muller-Landau et al. (2008) calculated two estimates for α (the dispersal distance parameter in a 2Dt distribution); in these cases, we used data that was fit to seed-fall data rather than fruit.

Our model predicts that the dispersal kernel of density-responsive enemies is equal to the seed dispersal kernel. Thus, for density-responsive enemies, $\widetilde{d_j d_{\mathrm{P},j}}$ is $\widetilde{d_j^2}$. So, we first calculated $d_j(z)$ for each species, for a distance between 0 and 8 (we still assumed that trees would take up approximately a 10×10m area). Instead of using Eq. 75, which relied on Manhattan distances, we used the following formula:

$$d_j(z)=\begin{cases}\frac{4}{\pi}\int_0^{l/2}D(y)dy & z=0\\ \frac{1}{(2\pi z)}\int_{l(z-0.5)}^{l(z+0.5)}D(y)dy & z\geq 1\end{cases} \qquad (82)$$

(with $D(y)$ in Eq. 74). For example, *Anacardium excelsum* has a dispersal parameter $\alpha_j=4.9$. Thus,

$$\begin{aligned}d_j(0)&=0.2002\\ d_j(1)&=0.0747\\ d_j(2)&=0.0157\\ d_j(3)&=0.0041\\ d_j(4)&=0.0015\\ d_j(5)&=0.0006\\ d_j(6)&=0.0003\\ d_j(7)&=0.0002\\ d_j(8)&=0.0001. \qquad (83)\end{aligned}$$

Next, we squared each term. Finally, we multiplied $d_j(z)^2$ by the area between $10(z-0.5)$ and $10(z+0.5)$ (i.e., 0.79, 6.28, 12.57, 18.85, 25.13, 31.42, 37.70, 43.98, and 50.27m^2), and summed those values. Thus, for *A. excelsum*, it is 0.07.

We found that across canopy trees, $\widetilde{d_j d_{\mathrm{P},j}}$ varies from 0.002 (*Zanthoxylum ekmanii*) to 0.193 (*Beilschmiedia pendula*), with a mean of $\overline{\widetilde{d_j d_{\mathrm{P},j}}}=0.057$. This suggests that in the absence of a dispersal-sensitivity trade-off, limited seed dispersal weakens the stabilizing effect of density-responsive enemies by about 6%. Future studies could improve this estimate by quantifying how p_j covaries with $\widetilde{d_j d_{\mathrm{P},j}}$, and whether more common species have higher $\widetilde{d_j d_{\mathrm{P},j}}$.

A6.3 Measuring dispersal-susceptibility trade-offs

In this subsection, we discuss how our model could be used to test for dispersal-susceptibility trade-offs.

At a basic level, a dispersal-susceptibility trade-off indicates that species that disperse their seeds farther are more susceptible to natural enemies. This could be done, by calculating each species' mean dispersal distance, or some similar parameter (e.g. α in a 2Dt distribution, Muller-Landau et al. (2008)), and correlating this with their potential CNDD (measured using techniques discussed in the main text). If the correlation is positive (i.e. species with

Table 4 Here we display data from Muller-Landau et al. (2008). We display only canopy trees, as classified by Comita et al. (2007). The parameter α_j is used for calculating a 2Dt distribution

Species name	α_j	$\widetilde{d_j d_{\mathrm{P},j}}$
Anacardium excelsum	4.9	0.07
Beilschmiedia pendula	3.84	0.193
Calophyllum longifolium	7.06	0.009
Chrysophyllum cainito	5.6	0.037
Cupania rufescens	6.51	0.015
Dendropanax arboreus	5.73	0.032
Dipteryx oleifera	4.74	0.081
Drypetes standleyi	4.61	0.092
Guapira standleyana	6.47	0.016
Guatteria dumetorum	6.33	0.018
Jacaranda copaia	5.8	0.03
Luehea seemannii	5.67	0.034
Platypodium elegans	4.96	0.066
Platymiscium pinnatum	4.5	0.102
Poulsenia armata	5.15	0.056
Pouteria reticulata	5.2	0.053
Pterocarpus rohrii	5.19	0.054
Quararibea asterolepis	4.24	0.131
Simarouba amara	6.02	0.025
Tabebuia guayacan	4.61	0.092
Tabebuia rosea	6.3	0.019
Terminalia amazonia	8.24	0.003
Tetragastris panamensis	4.8	0.077
Poulsenia armata	8.75	0.002
Trichilia tuberculata	3.93	0.177
Zanthoxylum ekmanii	8.4	0.002

higher dispersal are more susceptible), it indicates a trade-off is occurring. Indeed, this is essentially what we did in our simulations in Fig. 12. We are not currently aware of anyone who has done this.

Ideally, one would show that this trade-off is equalizing. This is somewhat complicated, as there is no good definition of "equalizing" in a multispecies community (Barabás et al. 2018). A mechanism is called equalizing if it reduces mean fitness-differences between species. In a two-species community, this is simple to calculate, as sp. 1's fitness is equal to negative sp. 2's fitness; thus, if a trade-off causes the absolute value of both decrease, it is equalizing. In a community with three or more species, however, this result is more complex.

With that caveat aside, we would suggest that the best way to see if this trade-off is equalizing is to check whether the trade-off affects the variance in mean fitness differences. The term ΔP_j will not contribute much to fitness-differences, $\Delta\kappa_{\mathrm{C}j}$ requires a huge number of parameters (and we worry the quantitative values in Eq. 71 may be model-specific), and $\Delta\kappa'_{\mathrm{C}j}$ and $\Delta\kappa'_{\mathrm{P}j}$ cannot be calculated reliably from parameters alone; therefore, we suggest focusing on $\Delta\kappa_{\mathrm{P}j}$. To do this, one would calculate $p_j\widetilde{d_j d_{\mathrm{P},j}}$ for each species, using methods described above, and determine its variance. Then, one would calculate what the variance of $p_j\widetilde{d_j d_{\mathrm{P},j}}$ is if all species had identical $\widetilde{d_j d_{\mathrm{P},j}}$. We would recommend setting $\widetilde{d_j d_{\mathrm{P},j}}$ to what $\widetilde{d_j d_{\mathrm{P},j}}$ would be if every species had the same mean seed dispersal, although an argument could be made for setting $\widetilde{d_j d_{\mathrm{P},j}}$ to the community-average value of $\widetilde{d_j d_{\mathrm{P},j}}$. In either case, if the variance is higher when species have identical $\widetilde{d_j d_{\mathrm{P},j}}$ values, then the trade-off is equalizing; otherwise it increases fitness differences.

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