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ARTICLE

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Competition–colonization dynamics and multimodality in diversity–disturbance relationships

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Abstract

Disturbance has long been recognized as a critical driver of species diversity in community ecology. Recently, it has been found that the well-known intermediate disturbance hypothesis, which predicts a unimodal diversity–disturbance relationship (DDR), fails to describe numerous experimental observations, as empirical DDRs are diverse. Consequently, the precise form of the DDR remains a topic of debate. Here we develop a simple yet comprehensive metacommunity framework that can account for complex competition patterns. Using both numerical simulations and analytical arguments, we show that strongly multimodal DDRs arise naturally, and this multimodality is quite robust to changing parameters or relaxing the assumption of a strict competitive hierarchy. Having multimodality as a robust property of DDRs in competition models suggests that much of the noise observed in empirical DDRs could be a critical signature of the underlying competitive dynamics.

KEYWORDS

competition–colonization tradeoff, diversity–disturbance relationship, intermediate disturbance hypothesis, linear time-averaged model, multimodal pattern, pairwise competition

INTRODUCTION

It is well established that disturbance plays an important role in maintaining biodiversity. The intermediate disturbance hypothesis (IDH) has been used as a critical explanation of biodiversity maintenance for several decades (Connell, 1978; dos Santos et al., 2011; Miller et al., 2011; Roxburgh et al., 2004; Sousa, 1984). In communities subject to the competition–colonization (C–C) tradeoff, the IDH postulates that species diversity peaks at intermediate levels of disturbance, yielding a unimodal diversity–disturbance relationship (DDR). However, there is considerable debate surrounding the IDH and its operation as a coexistence-promoting mechanism (Buckling et al., 2000; Cadotte, 2007; Hughes et al., 2007; Mackey & Currie, 2001; Scholes et al., 2005; Violle et al., 2010), as the evidence for the IDH appears mixed, and some explanations linking disturbance to species coexistence are flawed. Fox (2013) even argued that the IDH has been refuted on both theoretical and empirical grounds, and therefore it should be abandoned.

Instead of struggling to support or reject the IDH, we advocate shifting our focus to extending our understanding of the DDR. Recently, some empirical and theoretical studies have observed additional peaks in DDRs (Banitz et al., 2008; dos Santos et al., 2011; Hall et al., 2012; Johst & Huth, 2005; Lenz et al., 2004; Svensson et al., 2012), yet a systematic mechanistic explanation for this phenomenon is still lacking. In this study, we develop a simple, but comprehensive, pairwise competition model to characterize site-occupancy dynamics in multispecies systems subject to the C–C

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tradeoff, in order to systematically explore the factors that lead to the emergence of multiple peaks in DDRs.

METHODS

Generalized colonization–competition model

In classic C–C models (Adler & Mosquera, 2000; Hastings, 1980; Kinzig et al., 1999; Nee & May, 1992; Tilman, 1994), population dynamics are typically modeled using site occupancy. It is assumed that the landscape consists of a set of colony sites, and each site can only accommodate one individual of a species. Therefore, population size can be measured in terms of the number of colony sites that a species occupies, and population growth depends on the colonization–mortality dynamics. In addition, coexistence between competitors within a colony site is assumed to be impossible on the time scale of the model (Tilman, 1994). Therefore, competition is incorporated by assuming that colonizers of one species can displace individuals of other species (i.e., competitive displacement). The probability of competitive displacement is determined by the relative competition strength (H_{ij}) of the species involved (Li et al., 2020). We model an n-species system subject to colonization–mortality–competition processes with equations of the following form

$$\frac{dp_i}{dt} = \underbrace{c_i p_i \left(1-\sum_{j=1}^{n} p_j\right)}_{\text{Colonization}} \underbrace{-e_i p_i}_{\text{Mortality}} + \underbrace{\sum_{j=1}^{n} \left(c_i p_i H_{ij} p_j - c_j p_j H_{ji} p_i\right)}_{\text{Competition}}, \tag{1}$$

where p_i represents the fraction of sites occupied by species i, c_i is the colonization rate of species i, and e_i is its mortality rate. The colonization term describes the rate at which species are able to establish on empty sites, while competitive displacement is implemented via the competition term. In particular, competition occurs when colonizers (e.g., propagules) from one species ($c_i p_i$ or $c_j p_j$) arrive at a site occupied by another species and displace it. The parameters H_{ij} and H_{ji} are the independent probabilities that an individual of species i displaces species j and that species j displaces species i, respectively. These probabilities are encoded in a matrix H. The competition term is the sum of the net result of pairwise competition events, depending on the colonization pressure (i.e., $c_i p_i$) exerted by these species.

Compared with previous classic C–C tradeoff models with a strict competitive hierarchy (e.g., for plant communities; Shipley & Keddy, 1994; Tilman, 1994; Wilson et al., 2019), the generalized model presented here allows us to capture a much richer class of C–C dynamics (Li et al., 2020). In fact, existing models (Tilman, 1994) are a special case of our model, obtained by setting $H_{ij} = 1$ if $i < j$ and otherwise $H_{ij} = 0$ (Appendix S1: Section S1). In the generalized framework, both species i and j can invade into each other's colony sites with independent probabilities H_{ij} and H_{ji}, permitting much more complex competition structures to be described (e.g., competitive intransitivity; Allesina & Levine, 2011; Laird & Schamp, 2006, 2008; Li et al., 2020; Rojas-Echenique & Allesina, 2011).

If all species are assumed to have the same colonization rate $c_i = 1$, the competition term in Equation (1) becomes $p_i \sum_{j=1}^{n} (H_{ij} - H_{ji}) p_j$, which is superficially similar to the model of Grilli et al. (2017). However, in their model, all sites are assumed to be always occupied; when one site becomes empty due to mortality, a pair of randomly chosen individuals immediately competes to fill that site. Therefore, these interactions form a zero-sum tournament, that is, $H_{ij} + H_{ji} = 1$, as the probability of one of the two competing individuals filling the gap is 1. Importantly, our model does not necessarily follow this restriction, as the competition occurs between an invader and a resident (i.e., competitive displacement), instead of competing for an empty site. Therefore, the competition term in Equation (1) does not necessarily encode a zero-sum tournament. For instance, $H_{ij} = H_{ji} = 0$ simply means that there is a priority effect: whichever of species i or j is able to seize a site first will stay there and cannot be displaced by the other species.

The model under disturbance

According to Miller et al. (2021), the disturbance regime is characterized by both disturbance extent (D) and frequency $1/T$ (T – disturbance periodicity), that is, a given fraction D of each species is removed every T time units through elevated mortality rates. This can be conceived of as a sudden reduction in species' site occupancies occurring periodically (pulse disturbance; Bender et al., 1984; Liao et al., 2016). While other forms of disturbance are possible, for example, with alternative shapes or which are not strictly periodic, we observe that these variations have little effect on our conclusions (Appendix S2: Section S1). The generalized C–C model under disturbance is the same as in Equation (1), but adding a forcing term:

$$\frac{dp_i}{dt} = c_i p_i\left(1-\sum\nolimits_{j=1}^{n} p_j\right) - e_i p_i + \sum\nolimits_{j=1}^{n}\left(c_i p_i H_{ij} p_j - c_j p_j H_{ji} p_i\right) + f(t,D,T)p_i, \qquad (2)$$

where $f(t,D,T)$ is a forcing function, ensuring that a fraction D of each species is removed within every period T. We rearrange Equation (2) as:

$$\frac{dp_i}{dt} = p_i\left[\underbrace{c_i - e_i + f(t,D,T)}_{b_i} + \sum\nolimits_{j=1}^{n}\underbrace{(c_iH_{ij} - c_jH_{ji} - c_i)}_{A_{ij}}p_j\right], \qquad (3)$$

where b_i is the effective intrinsic growth rate of species i, A_{ij} is the effective interaction coefficient, and the bracketed term above is the per-capita growth rate $r_i = \frac{1}{p_i}\frac{dp_i}{dt}$ of species i. In such case, the per-capita growth rate is manifestly linear in p_i, and has the Lotka–Volterra form $r_i = b_i + \sum_{j=1}^{n} A_{ij}p_j$. This linearity allows one to take the time average of the per-capita growth rate directly:

$$\bar{r}_i = \bar{b}_i + \sum\nolimits_{j=1}^{n} A_{ij}\bar{p}_j, \qquad (4)$$

where the over-bar denotes time averaging. If we simply replace the fluctuating model with the one in which parameters are set to their time averages obtained from the fluctuating model, the long-term outcomes will not change. Here, p_i drops to $(1-D)p_i$ during every period T, therefore we set $f(t,D,T) = log(1-D)/T$, which gives the same long-term average result as the periodically disturbed model (please refer to explanation in Appendix S2: Section-S1). Due to the time averaging, the steady state is now characterized by setting all average per-capita growth rates equal to zero (i.e., $\bar{r}_i = 0$). At this steady state, we can express the patch occupancy of species i explicitly by inverting the matrix A:

$$\bar{p}_i^* = -\sum\nolimits_{j=1}^{n}\left(A^{-1}\right)_{ij}\left[c_j - e_j + log(1-D)/T\right], \qquad (5)$$

where $(A^{-1})_{ij}$ is the (i,j)th entry of A's inverse. Equation (5) gives the average stationary patch occupancies in response to a disturbance of extent D and frequency $1/T$ (please refer to more details in Appendix S2: Section S1). As our equations are linear in the per-capita growth rates and p_i does not multiply any time-dependent terms, the disturbed model's long-term behavior is identical to that of the time-averaged model (Barabás et al., 2018; Chesson, 1994; Kondoh, 2001; Svensson et al., 2012; Worm et al., 2002). In this non-fluctuating system, the linearity allowing simple time averaging is a very useful approach to gain numerical tractability and make our simulations considerably faster.

In this study, we focus on the DDR at equilibrium in an n-species system subject to the C–C tradeoff that has been often used to test IDH (Cadotte, 2007; Shea et al., 2004; Violle et al., 2010). We assume a competitive hierarchy by ranking the species from the best competitor (species 1) to the poorest (species n), and set species colonization rates as $c_1 < c_2 < c_3 < \ldots < c_n$ in order to establish the possibility of C–C tradeoffs. In addition to species richness, we use the Shannon index ($-\sum q_i log q_i$) to characterize species diversity, with $q_i = p_i / \sum p_j$ being the relative abundance of species i. To ensure that our results are not an artifact of the diversity index used, we also use the inverse Simpson index ($1/\sum q_i^2$) to measure species diversity. These indices are superior to raw species richness as measures of species diversity, because they consider the separate effects of species richness and evenness and their inter-relations (Banitz et al., 2008; dos Santos et al., 2011; Stirling & Wilsey, 2001).

For each parameterization, we integrate our model numerically using a backward differentiation formula. This is aided by the fact that disturbances can be analytically averaged over, eliminating any explicit time dependence from the equations (Appendix S2: Section S1). According to local and global stability analysis of feasible equilibria (Appendix S3: Section S1), the species either converge to a stable fixed point or form a stable limit cycle around a locally unstable equilibrium point. Furthermore, one can prove the existence of a globally stable fixed point whenever the species can be unambiguously arranged in a competitive hierarchy (Appendix S3: Section S1). Regardless of dynamical behavior, initial species abundances do not affect system steady state. To find the steady state, initially each case is run for a long time. Based on numerous preliminary trials, 15,000 time units (each time unit is approximately one generation in terms of life-history parameters) are sufficient for all cases to achieve steady state. Therefore, we run each case for 20,000 time units to eliminate initial transients, and use the time-averaged patch occupancies during the final 5000 time units for calculating diversity indices at steady state (please refer to code in Data S1).

RESULTS

We first implement a basic numerical simulation of our model (Appendix S3: Section S1) with several different multispecies communities, subject to the C–C tradeoff (please refer to parameter setting in Table 1). As seen in Figure 1, how many species can coexist without involving

TABLE 1 Analyses of the disturbed model at fixed frequency $1/T = 1$. $E[a, b]$ and $U[a, b]$ separately represent evenly spaced distribution and uniform distribution, with minimum a and maximum b

Simulations	Species richness	Mortality rates	Spread of colonization rates	Competitive matrix	Figures
Case 1	$n = 3, 4, 5, 6$	$e_i = 0.2$	$c_i \in E[0.25, 1]$ or $E[0.45, 0.8]$	$H_{ij} = 0$ or 1	1 and 2
Case 2	$n = 3, 4, 5, 6$	$e_i = 0.2$	$c_i \in E[0.45, 0.8]$	$H_{ij} \in U[0.75, 1]$ or $U[0, 0.25]$	3
			$c_i \in U[0.45, 0.8]$	$H_{ij} = 0$ or 1	
Case 3	$n = 25$	$e_i = 0.2$	$c_i \in U[0.25, 1]$ or $U[0.45, 0.8]$	$H_{ij} \in U[0.9, 1]$ or $U[0, 0.1]$	4

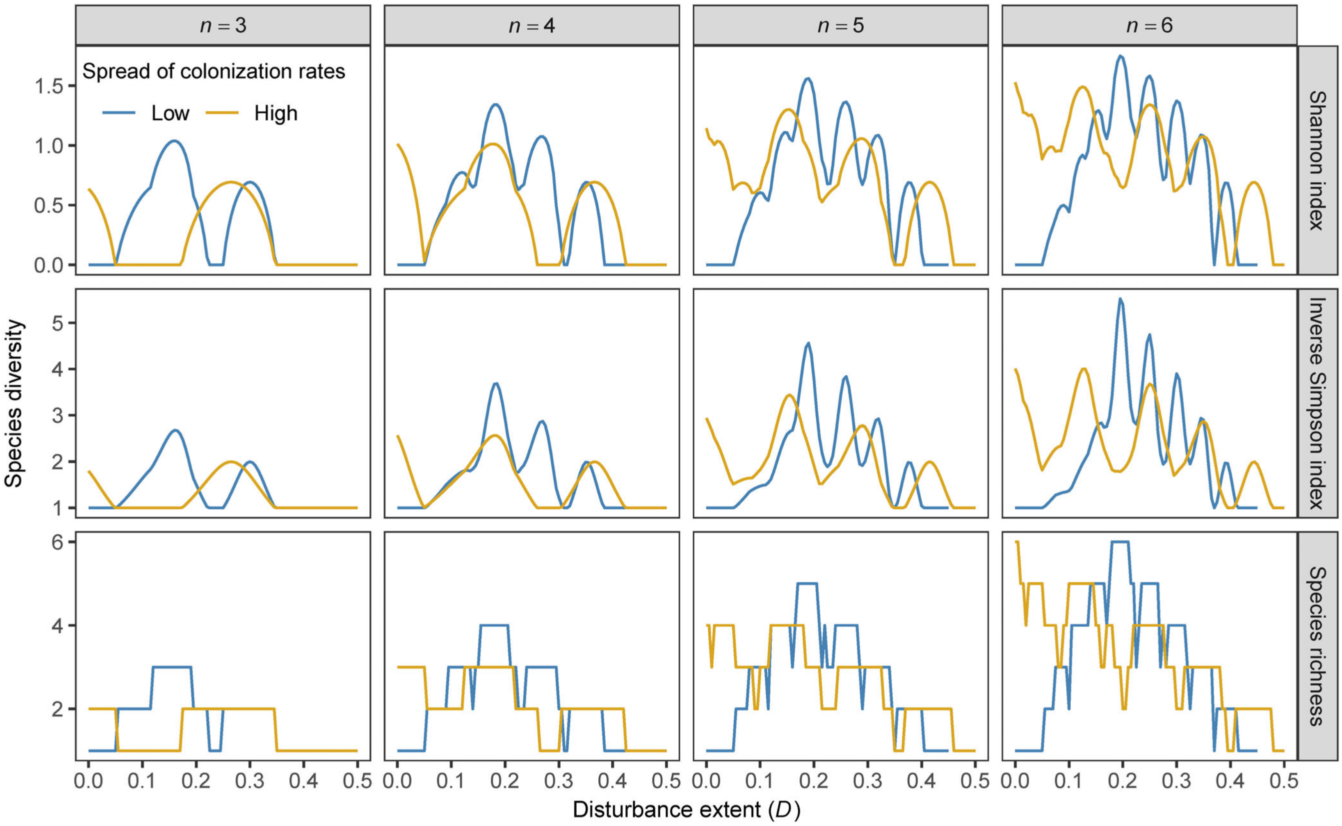

FIGURE 1 Diversity–disturbance curves in multispecies systems ($n = 3, 4, 5$, or 6), with a strict competitive hierarchy by ranking the species from the best competitor (species 1) to the poorest (species n), that is, a matrix H with $H_{ij} = 1$ for $i < j$ and 0 otherwise. Species diversity is characterized using richness, the Shannon index, and the inverse Simpson index. Other parameters: species mortality rates $e_i = 0.2$, and colonization rates c_i are evenly spaced in both low (blue lines: $c_i \in [0.45, 0.8]$) and high (yellow lines: $c_i \in [0.25, 1]$) spreads with a mean of $\bar{c} = 0.625$

disturbance ($D = 0$) depends on parameter combinations (including community size and variation in species colonization rates). For example, in the community of $n = 6$ species, only the best competitor dominates the system at a low spread of colonization rates, while all species can co-occur stably at a high spread of colonization rates simply due to the formation of the classic C–C tradeoff (cf. Tilman, 1994). Yet, as the disturbance extent increases, the diversity pattern is strongly oscillatory, regardless of community size. This means that we observe multiple peaks in the DDR, with more peaks emerging in species-richer communities. While both the Shannon and inverse Simpson indices oscillate, species richness does not always do so because of its insensitivity to species' relative abundances (species evenness; Appendix S5: Figure S2). The number of diversity peaks emerging in a given community strongly depends on parameterization, for example, a low spread of colonization rates generally shapes more peaks in species diversity than a high spread of colonization rates (Figure 1). We further observed that obtaining maximal diversity at intermediate disturbance extent is not guaranteed.

Looking at species' relative abundances at equilibrium as a function of the disturbance extent (Figure 2; Appendix S5: Figures S1, S3, S4), we illustrate why

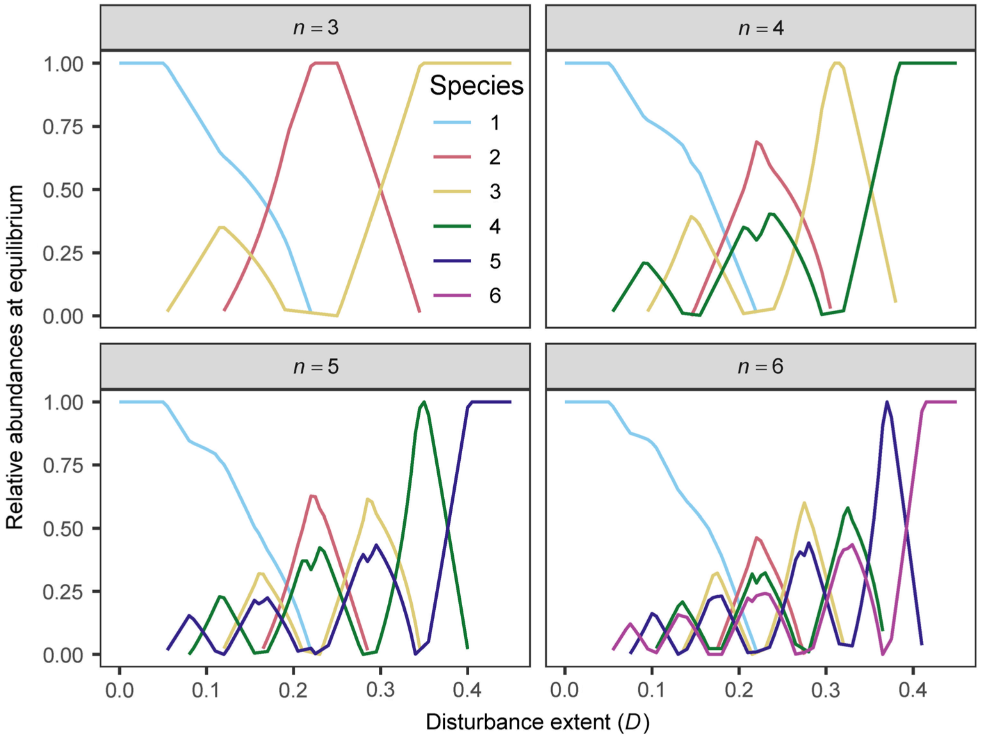

FIGURE 2 Effect of disturbance extent on species relative abundances in multispecies communities ($n = 3, 4, 5, 6$; species denoted by color lines) with a strict competitive hierarchy ($H_{ij} = 1$ for $i < j$ and 0 otherwise), mortality rates $e_i = 0.2$, and colonization rates c_i evenly spaced in $c_i \in [0.45, 0.8]$

multiple peaks emerge in the DDRs. The disturbance level at which a species either enters or leaves the system is a "turning point," that is, those low-abundance species that have been declining now start to increase, while high-abundance species begin to decrease, thereby creating a zig-zag pattern. Specifically, whenever some species are high in relative abundance but others are low, species diversity is low due to extreme unevenness. Conversely, whenever species' relative abundances are more equal, species diversity is boosted by high evenness. Therefore, it is natural that such a pattern would translate to an oscillating diversity profile. The alternating pattern in Figure 2 can be explained mathematically in terms of how the equilibrium average site occupancies $\overline{p}_i^*$ respond to a change in the disturbance extent (Appendix S4: Section S1). The peaks and troughs in the DDRs are a function of the pattern in which the species are "replacing" themselves along the disturbance gradient. In particular, the fact that approximately half of the species at any point along the disturbance extent axis are increasing and the other half are decreasing in frequency, is what causes the clear oscillations in the diversity indices. Without such a "synchrony" along the disturbance extent (e.g., if species respond more individualistically to an increase in D), one would observe a different looking DDR.

The effects of disturbance depend not only on its extent D, but also on its periodicity T (the average time between two subsequent disturbance events), which is fixed at $T = 1$. However, in our model, the effects of a disturbance with extent D and period T are equivalent to the effects of another disturbance with extent $D' = 1-(1-D)^{1/T}$ and periodicity $T' = 1$ (Appendix S2: Figure S1). Therefore, varying D alone, while keeping $T = 1$, is sufficient for gaining a full understanding of the impact of disturbance.

Up to this point, we have operated with a set of stringent assumptions: a full competitive hierarchy (better competitors always win against weaker ones), evenly spaced colonization rates, and a small number of species. However, our numerical results are robust, even when these assumptions are relaxed (please refer to Table 1). In particular, we continue to obtain multimodal DDRs for systems without a strict competitive hierarchy (Figure 3, blue curves; Appendix S5: Figures S5, S7), systems with irregularly spaced colonization rates (Figure 3, yellow curves; Appendix S5: Figure S5), and significantly larger initial communities ($n = 25$, Figure 4; Appendix S5: Figures S6, S7). As such, one can expect these results to hold across a broad range of model configurations.

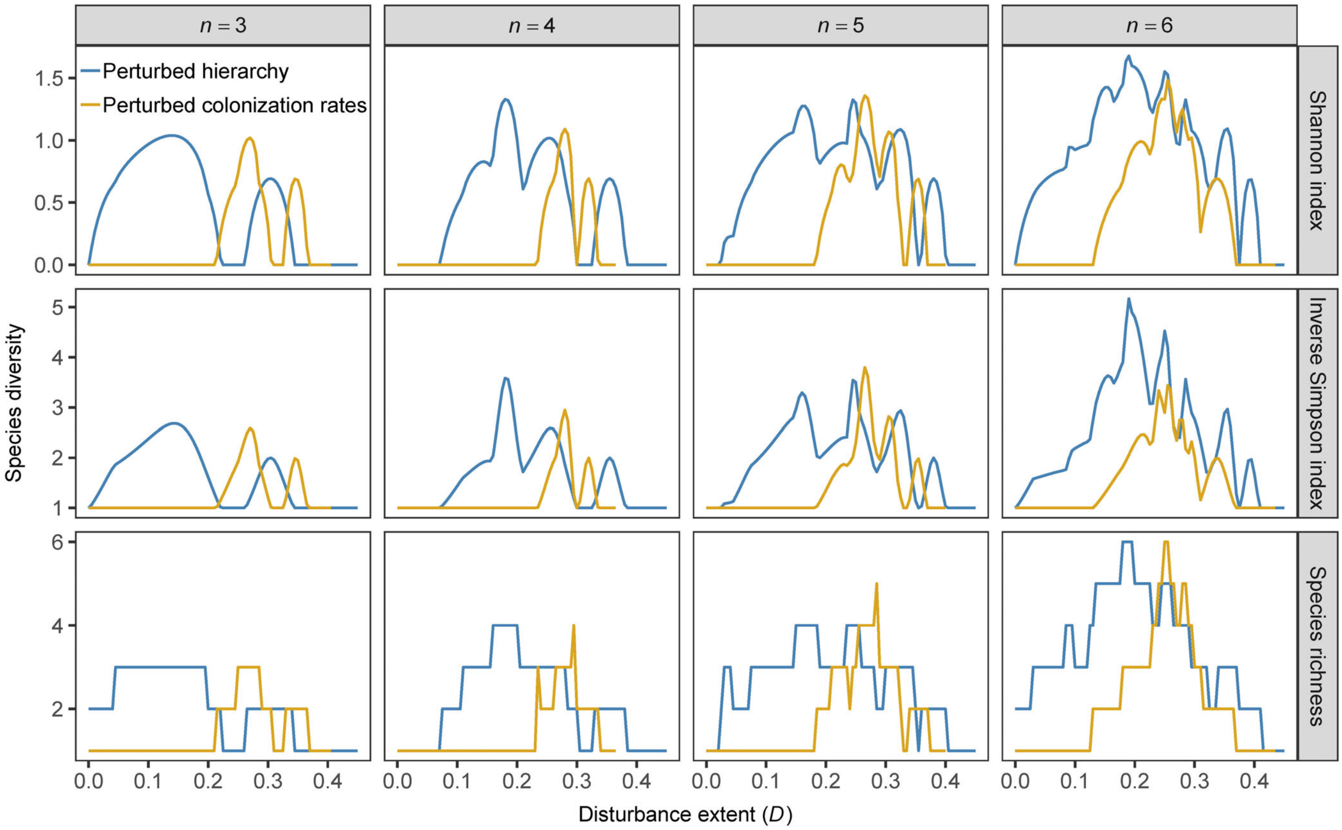

FIGURE 3 Diversity–disturbance curves in multispecies systems, considering two cases. First, colonization rates are evenly spaced in $c_i \in [0.45, 0.8]$ while weakening the competitive hierarchy H: the upper and lower triangular entries are uniformly sampled from [0.75, 1] and [0, 0.25] respectively (blue lines). Second, colonization rates c_i are uniformly drawn from [0.45, 0.8] and sorted in increasing order, but with a strict competitive hierarchy H (yellow lines). Others: please refer to Figure 1

DISCUSSION

We demonstrate that multiple diversity peaks emerge naturally along the disturbance gradient, shaping multimodal DDRs. This suggests that the prevailing assumption of a unimodal DDR, as predicted by the IDH (Connell, 1978; Roxburgh et al., 2004; Sousa, 1984), fails to capture the full complexity of the DDR. Furthermore, the emergence of multimodal patterns is a consistent feature of our results, indicating that it is a relatively generic feature of DDRs arising from C–C dynamics.

In the C–C tradeoff communities, more damaging disturbance regimes increase the number of unoccupied sites, favoring species with high colonization rates. Consequently, disturbance promotes the survival of weaker competitors that would otherwise be excluded by the best competitor. Furthermore, a continuous increase in the disturbance extent would facilitate distinct subsets of weak competitors to coexist, thereby creating multiple peaks in the DDR. For instance, in a simple three-species system (Figures 1 and 2), the best competitor monopolizes the landscape at low disturbance levels. As the disturbance extent increases, the relative abundance of the best competitor declines, allowing first the poorest competitor (best colonizer) and later the intermediate competitor to increase in abundance. This results in an increase in species diversity. With further increasing the disturbance extent, the best competitor continues to decline, reducing competition pressure on the intermediate competitor. Therefore, the abundance of the intermediate competitor increases, which in turn increases competition pressure on the poorest competitor, leading to a decline of this species and therefore diversity. Consequently, a diversity peak forms in this range. Eventually, the best competitor becomes extinct, forming a two-species system, in which the strong competitor (previously intermediate) declines and the poor competitor increases, as, again, colonization rate becomes the dominant factor in determining species abundance. This forms a second diversity peak when the two species have equal abundances, which decays as the poor competitor (strong colonizer) comes to dominate. In the multispecies communities ($n > 3$) with the C–C tradeoff, an increase of disturbance extent would decrease the abundance of the

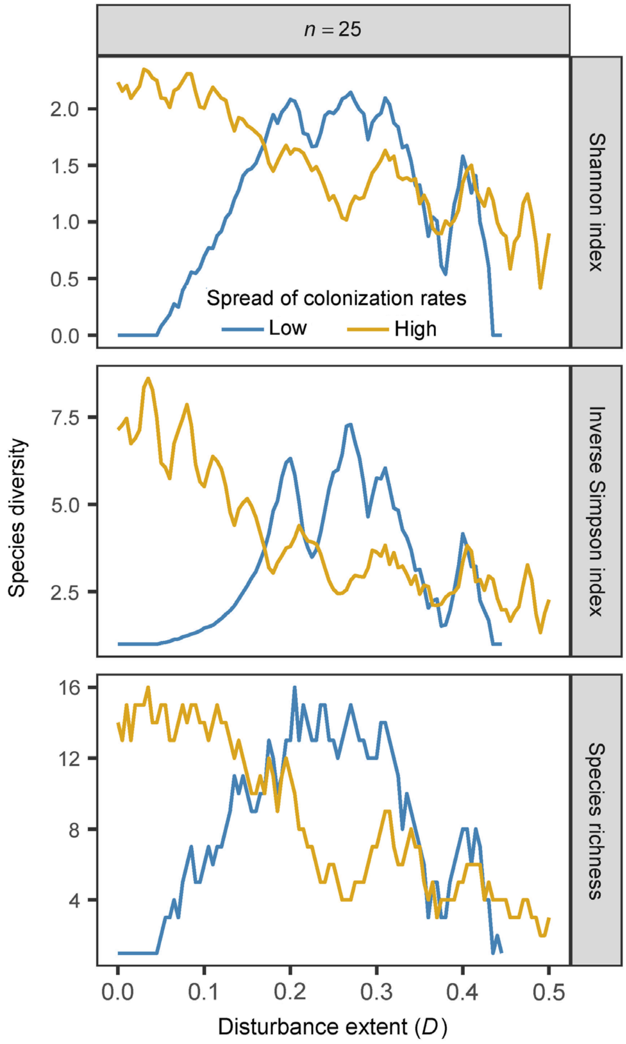

FIGURE 4 Diversity–disturbance curves in a community of $n = 25$, with a small perturbed competitive hierarchy H: the upper and lower triangular entries are uniformly sampled from [0.9, 1] and [0, 0.1] respectively. Colonization rates c_i are uniformly drawn from both low (blue lines: $c_i \in [0.45, 0.8]$) and high (yellow lines: $c_i \in [0.25, 1]$) spreads, and sorted in increasing order. Mortality rates are $e_i = 0.2$ for all species

best competitor (species 1) due to the lowest colonization rate, eventually leading to species 1 becoming extinct first. The decline in species 1 affects the second superior competitor (species 2) positively, species 3 negatively, species 4 positively again, and so on. Yet, the extinction of species 1 would reduce species 2, increase species 3, reduce species 4, etc., resulting in a sharp change in the trajectories of all species abundances at equilibrium as a function of increasing the disturbance extent. If the effect is strong enough to not just change the trajectory but turn increasing ones into decreasing ones and vice versa, then the patterns of species relative abundances shown in Figure 2 are established (please refer to system analysis in Appendix S4: Section S1). Therefore, these processes would repeat more times in larger communities, resulting in the multimodality in DDRs.

It is important to clarify the role that temporal disturbances play in our model. We construct the disturbed model as the time-averaged model by adjusting the per-capita growth rates to account for the mean effect of disturbances (e.g., Kondoh, 2001; Svensson et al., 2012; Worm et al., 2002). This means that storage effects or relative nonlinearities cannot arise (Fox, 2013) and, as such, that the patterns we observe do not emerge from such mechanisms. Instead, our disturbance regime changes the effective long-term mortality rates of the species, altering the time-averaged equilibrium point. Similarly, the increased mortality due to disturbance will result in the negative intrinsic growth of the best competitor (with the lowest colonization rate) before other species, and its extinction will suddenly alter the direction of the trajectories in the equilibrium abundances of the remaining species. Repeating this process as the disturbance extent increases, would therefore form the multimodal patterns. However, in this context, the time-averaged equilibrium should be interpreted as a balance point of the succession dynamics of the system (Fox, 2013). In particular, while the proportions of species in this equilibrium are constant, they arise from an ongoing cycle of extinctions, caused by disturbances and site recolonizations.

Disturbances increase the effective long-term mortality rates of species in our C–C model. This disproportionately affects species that would persist for the longest times in an undisturbed system, that is, the strong competitors that are able to displace weaker competitors (stronger colonizers). As a result, an intermediate disturbance range exists, that is, where neither strong competition nor strong colonization strategies dominate, which allows disturbances to act as an equalizing rather than a stabilizing mechanism (Chesson, 2000; Chesson & Huntly, 1997). In such regimes, both strategies have similar chances to succeed, and once species of either type drop to low levels of abundance they are unable to recover. At low or high levels of disturbance, strong competitors or strong colonizers respectively gain an advantage and exclude species following the other strategy.

Previous studies have often confused the effects of disturbance on the long-term average morality rate with effects arising from fluctuations in the mortality rate. In fact, long-term average conditions, and fluctuations around the average, can vary independently of one another in nature. In our model, fluctuations around the average per-capita mortality rates cancel out, so that, in the long term, growth rates depend only on the average values of these parameters. Such fluctuations in mortality can produce fluctuations in the abundances of species but, unless stronger competitors experience stronger fluctuations, do not create the stabilizing effect required for producing stable coexistence (i.e., fluctuation-dependent mechanism; Chesson & Huntly, 1997). Therefore, it is very important to distinguish between the effects of changes in the average long-term mortality rate from the effects of variation in mortality rates around a fixed mean.

Although the DDR has been studied extensively in experiments, so far no consensus on its expected shape has been reached, as empirical DDRs are messy. Mackey and Currie (2001) conducted a meta-analysis of empirical disturbance studies, finding that, in addition to the unimodal hump-shaped pattern predicted by the IDH, other DDRs (including monotonically declining, monotonically increasing, and even U-shaped) are also commonly found in nature. Miller et al. (2011) modeled the interactive effects of disturbance intensity and frequency on DDRs in a two-species system for annual plants, similarly finding various shapes of DDRs. Therefore, both empirical and theoretical findings are in stark contrast with the IDH, suggesting that unimodal DDRs may not be the rule. More importantly, our model provides a new multimodal DDR paradigm, offering a mechanistic explanation for the diversity of DDRs observed in nature, as it is able to produce all types of DDR described above. In addition, some empirical work have actually observed multiple diversity peaks along the disturbance gradient (Cadotte, 2007; Gibbons et al., 2016; Hall et al., 2012; Lenz et al., 2004), demonstrating that the predicted multimodality in DDRs might hold across a wide range of real ecosystems.

To date, such multimodal patterns have typically been ignored in some empirical work, for several reasons. First, experimental studies often tried to take several levels of disturbance or a small range of disturbance as representative of the effect of its full range, therefore neglecting regimes that could drive the emergence of more complex community dynamics. Second, even when a full range of disturbance regimes was considered, experiments may have been designed with insufficient statistical power to detect multimodal patterns, particularly when there is unexpectedly high variation. Finally, some field experiments, typically conducted in terrestrial plant communities within a single growing season, cannot observe competitive exclusion or stable species coexistence (Shea et al., 2004). Consequently, these studies are not suitable to establish the complete linkage between disturbance and C–C tradeoffs. Despite these limitations, those observed general patterns that are either monotonically declining or hump shaped (Cadotte, 2007; Gao & Carmel, 2020; Hall et al., 2012; Violle et al., 2010), are highly consistent with the overall DDRs we predict, suggesting that higher resolution experiments could directly capture the multimodality in DDRs.

For simplicity, we use the linear time averaging model to simulate the mean effect of disturbances. This is relatively restrictive, as a wealth of evidence suggests that larger, rarer disturbances are not equivalent to more common, smaller disturbances with the same "rate" (e.g., Miller et al., 2012). In addition, our disturbed model ignores the coexistence mechanisms of relative nonlinearities and storage effects that might be common in nature (Chesson, 2000). Relative nonlinearity, which acts when species' growth rates respond differently and nonlinearly to competition under a fluctuating environment, can allow multiple competitors to coexist stably, as the superior competitors' average population growth rates are significantly depressed as a result of disturbance (Chesson, 1994, 2000; Roxburgh et al., 2004). The storage effect in turn can be conceptualized as temporal niche segregation: different species specialize in different phases of the environmental fluctuations, allowing them to survive unfavorable periods (Barabás et al., 2018; Chesson, 1994, 2000; Chesson & Huntly, 1997; Fox, 2013; Miller et al., 2011; Roxburgh et al., 2004; Shea et al., 2004). It is an open question whether there are circumstances under which the above fluctuation-dependent mechanisms have a strong influence on the DDR, and how common those circumstances are. We also do not know how the DDR would be influenced in such cases. This is an avenue for further exploration, which could be done by extending the model to allow for coexistence-promoting nonlinearities (e.g., the type II functional response in prey–predator systems; Armstrong & McGehee, 1980; Fox, 2013), or storage effects (e.g., by making the entries of the matrix H fluctuation-dependent).

Despite these limitations, the simplicity of our generalized C–C framework offers the opportunity to validate the multimodality in DDRs, for example, using both microcosm experiments (Buckling et al., 2000; Gibbons et al., 2016; Kassen et al., 2000; Violle et al., 2010) and field observations (e.g., comparative analysis along natural disturbance gradients; Castorani & Baskett, 2020; Garrison et al., 2012; Moloney & Levin, 1996; Worm et al., 2002; Zhang & Shea, 2012). In particular, microcosm experiments have the key advantage that the rapid microbial reproduction (e.g., protists) allows multigenerational community dynamics to be studied within short time frames (Gibbons et al., 2016; Violle et al., 2010). However, we note that it might be difficult to explore a sufficient range of disturbance regimes in artificial experiments. As such, it might be preferable to parameterize our model (please refer to derivations in Appendix S2: Section S1) from short-term data for specific systems and then use the parameterized model to infer the long-term average DDRs. Similar approaches have proven effective in many recent studies of species coexistence (Levine et al., 2017; Petry et al., 2018).

In conclusion, our generalized model generates robust multimodality in DDRs for hierarchical competitive systems. This emerges from the interaction of disturbance and C–C tradeoffs, which can facilitate specific subsets of species to coexist. The theoretical outcome might offer new insights into biodiversity conservation: introducing a specific disturbance to the system or altering an existing disturbance regime could be a useful strategy either to control species invasion or to promote species coexistence. Overall, this study provides a parsimonious explanation for the emergence of multiple peaks in species diversity, further enriching our understanding of DDRs in systems characterized by C–C dynamics.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Jinbao Liao conceived the study and wrote the first draft; Jinbao Liao, György Barabás and Daniel Bearup built the model and conducted model analysis, Jinbao Liao and György Barabás rewrote the manuscript; György Barabás wrote the R codes; Daniel Bearup contributed substantially to its revision.

DATA AVAILABILITY STATEMENT

No data were collected for this study. Novel code used to model diversity–disturbance relationships (Liao et al., 2022) is available on Zenodo at https://doi.org/10.5281/zenodo.5880417.

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REFERENCES

Adler, R. F., and J. Mosquera. 2000. “Is Space Necessary? Interference Competition and Limits to Biodiversity.” *Ecology* 81: 3226–32.

Allesina, S., and J. M. Levine. 2011. “A Competitive Network Theory of Species Diversity.” *Proceedings of the National Academy of Sciences of the United States of America* 108: 5638–42.

Armstrong, R. A., and R. McGehee. 1980. “Competitive Exclusion.” *American Naturalist* 115: 151–70.

Banitz, T., A. Huth, V. Grimm, and K. Johst. 2008. “Clumped Versus Scattered: How Does the Spatial Correlation of Disturbance Events Affect Biodiversity?” *Theoretical Ecology* 1: 231–40.

Barabás, G., R. D’Andrea, and S. M. Stump. 2018. “Chesson’s Coexistence Theory.” *Ecological Monographs* 88: 277–303.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. “Perturbation Experiments in Community Ecology - Theory and Practice.” *Ecology* 65: 1–13.

Buckling, A., R. Kassen, G. Bell, and P. B. Rainey. 2000. “Disturbance and Diversity in Experimental Microcosms.” *Nature* 408: 961–4.

Cadotte, M. W. 2007. “Competition–Colonization Trade-Offs and Disturbance Effects at Multiple Scales.” *Ecology* 88: 823–9.

Castorani, M. C. N., and M. L. Baskett. 2020. “Disturbance Size and Frequency Mediate the Coexistence of Benthic Spatial Competitors.” *Ecology* 101: e02904.

Chesson, P. 1994. “Multispecies Competition in Variable Environments.” *Theoretical Population Biology* 45: 227–76.

Chesson, P., and N. Huntly. 1997. “The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities.” *American Naturalist* 150: 519–53.

Chesson, P. 2000. “Mechanisms of Maintenance of Species Diversity.” *Annual Review of Ecology, Evolution, and Systematics* 31: 343–66.

Connell, J. H. 1978. “Diversity in Tropical Rain Forests and Coral Reefs.” *Science* 199: 1302–10.

dos Santos, F. A. S., K. Johst, and V. Grimm. 2011. “Neutral Communities May Lead to Decreasing Diversity-Disturbance Relationships: Insights from a Generic Simulation Model.” *Ecology Letters* 14: 653–60.

Fox, J. W. 2013. “The Intermediate Disturbance Hypothesis Should Be Abandoned.” *Trends in Ecology & Evolution* 28: 86–92.

Gao, J., and Y. Carmel. 2020. “Can the Intermediate Disturbance Hypothesis Explain Grazing-Diversity Relations at a Global Scale?” *Oikos* 129: 493–502.

Garrison, A., A. Miller, S. H. Roxburgh, and K. Shea. 2012. “More Bang for the Land Manager’s Buck: Disturbance Autocorrelation Can Be Used to Achieve Management Objectives at No Additional Cost.” *Journal of Applied Ecology* 49: 1020–7.

Gibbons, S. M., M. Scholz, A. L. Hutchison, A. R. Dinner, J. A. Gilbert, and M. L. Coleman. 2016. “Disturbance Regimes Predictably Alter Diversity in an Ecologically Complex Bacterial System.” *mBio* 7: e01372-16.

Grilli, J., G. Barabás, M. J. Michalska-Smith, and S. Allesina. 2017. “Higher-Order Interactions Stabilize Dynamics in Competitive Network Models.” *Nature* 548: 210–3.

Hall, A. R., A. D. Miller, H. C. Leggett, S. H. Roxburgh, A. Buckling, and K. Shea. 2012. “Diversity-Disturbance Relationships: Frequency and Intensity Interact.” *Biology Letters* 8: 768–71.

Hastings, A. 1980. “Disturbance, Coexistence, History, and Competition for Space.” *Theoretical Population Biology* 18: 363–73.

Hughes, A. R., J. E. Byrnes, D. L. Kimbro, and J. J. Stachowicz. 2007. “Reciprocal Relationships and Potential Feedbacks between Biodiversity and Disturbance.” *Ecology Letters* 10: 849–64.

Johst, K., and A. Huth. 2005. “Testing the Intermediate Disturbance Hypothesis: When Will there Be Two Peaks of Diversity?” *Diversity and Distributions* 11: 111–20.

Kassen, R. A., A. Buckling, G. Bell, and P. B. Rainey. 2000. “Diversity Peaks at Intermediate Productivity in a Laboratory Microcosm.” *Nature* 406: 508–12.

Kinzig, A. P., S. A. Levin, J. Dushoff, and S. Pacala. 1999. "Limiting Similarity, Species Packing, and System Stability for Hierarchical Competition-Colonization Models." *American Naturalist* 153: 371–83.

Kondoh, M. 2001. "Unifying the Relationships of Species Richness to Productivity and Disturbance." *Proceedings of the Royal Society B* 268: 269–71.

Laird, R. A., and B. S. Schamp. 2006. "Competitive Intransitivity Promotes Species Coexistence." *American Naturalist* 168: 182–93.

Laird, R. A., and B. S. Schamp. 2008. "Does Local Competition Increase the Coexistence of Species in Intransitive Networks?" *Ecology* 89: 237–47.

Lenz, M., M. Molis, and M. Wahl. 2004. "Testing the Intermediate Disturbance Hypothesis: Response of Fouling Communities to Various Levels of Emersion Intensity." *Marine Ecology-Progress Series* 278: 53–65.

Levine, J. M., J. Bascompte, P. B. Adler, and S. Allesina. 2017. "Beyond Pairwise Mechanisms of Species Coexistence in Complex Communities." *Nature* 546: 56–64.

Li, Y., D. Bearup, and J. Liao. 2020. "Habitat Loss Alters Effects of Intransitive Higher-Order Competition on Biodiversity: A New Metapopulation Framework." *Proceedings of the Royal Society B* 287: 20201571.

Liao, J., Z. Ying, D. A. Woolnough, A. D. Miller, Z. Li, and I. Nijs. 2016. "Coexistence of Species with Different Dispersal across Landscapes: A Critical Role of Spatial Correlation in Disturbance." *Proceedings of the Royal Society B* 283: 20160537.

Liao, J., G. Barabás, and D. Bearup. 2022. "Competition-Colonization Dynamics and Multimodality in Diversity-Disturbance Relationships." Zenodo, Code. https://doi.org/10.5281/zenodo.5880417

Mackey, R. L., and D. J. Currie. 2001. "The Diversity–Disturbance Relationship: Is it Generally Strong and Peaked?" *Ecology* 82: 3479–92.

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. "How Frequency and Intensity Shape Diversity-Disturbance Relationships." *Proceedings of the National Academy of Sciences of the United States of America* 108: 5643–8.

Miller, A. D., R. Dan, S. Bauman, and K. Shea. 2012. "Interactions between Frequency and Size of Disturbance Affect Competitive Outcomes." *Ecological Research* 27: 783–91.

Miller, A. D., H. Inamine, A. Buckling, S. H. Roxburgh, and K. Shea. 2021. "How Disturbance History Alters Invasion Success: Biotic Legacies and Regime Change." *Ecology Letters* 24: 687–97.

Moloney, K. A., and S. A. Levin. 1996. "The Effects of Disturbance Architecture on Landscape-Level Population Dynamics." *Ecology* 77: 375–94.

Nee, S., and R. M. May. 1992. "Dynamics of Metapopulations: Habitat Destruction and Competitive Coexistence." *Journal of Animal Ecology* 61: 37–40.

Petry, W. K., G. S. Kandlikar, N. J. B. Kraft, O. Godoy, and J. M. Levine. 2018. "A Competition-Defence Trade-Off Both Promotes and Weakens Coexistence in an Annual Plant Community." *Journal of Ecology* 106: 1806–18.

Rojas-Echenique, J. R., and S. Allesina. 2011. "Interaction Rules Affect Species Coexistence in Intransitive Networks." *Ecology* 92: 1174–80.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. "The Intermediate Disturbance Hypothesis: Patch Dynamics and Mechanisms of Species Coexistence." *Ecology* 85: 359–71.

Scholes, L., P. H. Warren, and A. P. Beckerman. 2005. "The Combined Effects of Energy and Disturbance on Species Richness in Protist Microcosms." *Ecology Letters* 8: 730–8.

Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. "Moving from Pattern to Process: Coexistence Mechanisms under Intermediate Disturbance Regimes." *Ecology Letters* 7: 491–508.

Shipley, B., and P. A. Keddy. 1994. "Evaluating the Evidence for Competitive Hierarchies in Plant Communities." *Oikos* 69: 340–5.

Sousa, W. P. 1984. "The Role of Disturbance in Natural Communities." *Annual Review of Ecology, Evolution, and Systematics* 15: 353–91.

Stirling, G., and B. Wilsey. 2001. "Empirical Relationships between Species Richness, Evenness, and Proportional Diversity." *American Naturalist* 158: 286–99.

Svensson, J. R., M. Lindegarth, P. R. Jonsson, and H. Pavia. 2012. "Disturbance-Diversity Models: What Do They Really Predict and How Are They Tested?" *Proceedings of the Royal Society B* 279: 2163–70.

Tilman, D. 1994. "Competition and Biodiversity in Spatially Structured Habitats." *Ecology* 75: 2–16.

Violle, C., Z. Pu, and L. Jiang. 2010. "Experimental Demonstration of the Importance of Competition under Disturbance." *Proceedings of the National Academy of Sciences of the United States of America* 107: 12925–9.

Wilson, J. B., A. D. Q. Agnew, and S. H. Roxburgh. 2019. "Mechanisms of Coexistence." In *The Nature of Plant Communities*, edited by J. B. Wilson, A. D. Q. Agnew, and S. H. Roxburgh, 66–104. Cambridge: Cambridge University Press.

Worm, B., H. Lotze, H. Hillebrand, and U. Sommer. 2002. "Consumer Versus Resource Control of Species Diversity and Ecosystem Functioning." *Nature* 417: 848–51.

Zhang, R., and K. Shea. 2012. "Integrating Multiple Disturbance Aspects: Management of an Invasive Thistle, *Carduus nutans*." *Annals of Botany* 110: 1395–401.

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