

ARTICLE

Complex interactive responses of biodiversity to multiple environmental drivers

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Abstract

There remains considerable doubt, debate, and confusion regarding how biodiversity responds to gradients of important environmental drivers, such as habitat size, resource productivity, and disturbance. Here we develop a simple but comprehensive theoretical framework based on competition–colonization multispecies communities to examine the separate and interactive effects of these drivers. Using both numerical simulations and analytical arguments, we demonstrate that the critical trade-off between competitive and colonization ability can lead to complex nonlinear, zig-zag responses in both species richness and the inverse Simpson index along gradients of these drivers. Furthermore, we find strong interactions between these drivers that can dramatically shift the response of biodiversity to these gradients. The zig-zag patterns in biodiversity along ecological gradients, together with the strong interactions between the drivers, can explain the mixed findings of empirical studies and syntheses, thereby providing a new paradigm that can reconcile debates on the relationships between biodiversity and multiple drivers.

KEYWORDS

competition–colonization trade-off, disturbance, habitat size, multiple environmental drivers, resource productivity, zig-zag responses in biodiversity

INTRODUCTION

Despite centuries of study (Darwin, 1839; von Humboldt & Bonpland, 1807; Wallace, 1876), we still puzzle about some of the most basic patterns of biodiversity and how it varies across biogeographic and environmental gradients (Gaston, 2000; Rahbek et al., 2019; Rosenzweig, 1995; Willig et al., 2003). While general theories of biodiversity

abound (e.g., Hubbell, 2001; Huston, 1994; McGill, 2010; Storch & Okie, 2019; Worm & Tittensor, 2018), none capture the full magnitude of variation of biodiversity and its associations with biogeographic, environmental, or ecological factors observed in nature (Enquist et al., 2015; Rangel et al., 2018; Violle et al., 2014). Nevertheless, understanding the patterns and underlying drivers of biodiversity and its variation across gradients is

particularly imperative in light of ongoing anthropogenic stressors that alter the numbers of species across the planet, as well as their role in the functioning of ecosystems and services they provide to humans (Díaz et al., 2019).

Patterns of biodiversity vary across many ecological gradients, but three of the most prominent include habitat area (Chase et al., 2020; He & Hubbell, 2011; Pimm & Askins, 1995), resource productivity (Grime, 1973; Tilman, 1993; Worm et al., 2002), and disturbance (Connell, 1978; Roxburgh et al., 2004; Worm et al., 2002). Each of these drivers varies naturally across locations, but can also be altered by anthropogenic activities that can change patterns of diversity. For example, species diversity is usually presumed to increase with increasing area of an island or habitat-island (e.g., lake, mountain-top) (MacArthur & Wilson, 1967; Triantis et al., 2012) or decrease when habitats are destroyed to shape isolated patches (Chase et al., 2020; He & Hubbell, 2011; Matthews et al., 2019). We refer to this relationship as the island-type species–area relationship (island-type SAR; MacArthur & Wilson, 1967; Triantis et al., 2012). Note that this island-type SAR differs from a nested SAR, which displays a smoothly rising curve in continuous space (i.e., nondecreasing; Scheiner, 2003). The island-type SAR, however, can have more complex relationships with habitat area, showing complex nonmonotonic patterns (e.g., the wave-like increasing), and can even decrease, in both theory (Hastings, 1980; Nee & May, 1992; Tilman et al., 1997; Zhang et al., 2023) and observation (Bengtsson, 1991; Fahrig, 2017; Hanski & Ranta, 1983; Rosenzweig, 1995). Likewise, the relationship between drivers of primary productivity (e.g., water, nutrients, and/or energy) and species diversity, which we refer to as the productivity–diversity relationship (PDR), has been well studied, but there is no consensus of its general relationship. Instead, there is considerable evidence for diverse PDRs (including unimodal, positive, negative, and even no significant relationship) from both theory (Abrams, 1995; Guo, Barabás, et al., 2023; Kondoh, 2001; Pacala & Tilman, 1994) and empirical studies (Adler et al., 2011; Chase & Leibold, 2002; Fraser et al., 2015; Mittelbach et al., 2001; Waide et al., 1999). Finally, even though the disturbance–diversity relationship (DDR) is often thought to be unimodal based on classical “intermediate disturbance hypothesis” (Connell, 1978), both theory and empirical evidence remain mixed, with frequent evidence for other relationships (e.g., positive, negative, U-shaped or nonsignificant) (Fox, 2013; Liao et al., 2022; Mackey & Currie, 2001; Miller et al., 2011; Svensson et al., 2012). In short, we have consistently failed to find generality in the theoretically expected, or empirically

observed, form of three of the most important ecological gradients of biodiversity (i.e., SAR, PDR, and DDR).

There are several possible reasons for the complexity and debate regarding the SAR, PDR, and DDR. This can include the spatial scale in which diversity is measured (Chase & Leibold, 2002; Riva & Fahrig, 2023) and inherent differences in the nature by which species interact with their environment and each other (Genner et al., 2010; Hagen et al., 2012; Kissling et al., 2018; Thuiller et al., 2006). However, even when measured at the same scale and with similar parameters, patterns of SAR, PDR, and DDR can be highly variable. One reason for this variation is that habitat size, productivity, and disturbance do not act independently, but rather have interactive effects on biodiversity. For example, Dodson et al. (2000) found that the shape of the PDR in lakes depended on lake area. Likewise, disturbance and productivity can interact in important ways to influence biodiversity patterns in both theory (Huston, 1979, 1994; Kondoh, 2001) and empirical studies (Death & Zimmermann, 2005; Kneitel & Chase, 2004; Proulx & Mazumder, 1998; Scholes et al., 2005; Svensson et al., 2012). Indeed, natural communities are almost always subject to multiple environmental drivers simultaneously (Crain et al., 2008; Halpern et al., 2008; Tylianakis et al., 2008; Venter et al., 2006), and these interactions likely increase as a consequence of anthropogenic change. For example, habitat loss is a near-ubiquitous consequence of human activities, which simultaneously alter disturbance and resource regimes (Díaz et al., 2019). However, these drivers often interact in complex and unexpected ways (Crain et al., 2008; Dieleman et al., 2012; Jackson et al., 2016).

Another important reason for the lack of clarity on how environmental drivers influence patterns of biodiversity is that theoretical models often produce complex expectations. When species interact in multispecies communities, responses of species coexistence to drivers are often nonmonotonic (Hastings, 1980; Leibold, 1996; Liao et al., 2022; Nee & May, 1992; Tilman et al., 1997; Zhang et al., 2023). For example, along smooth gradients of disturbance or resources, the numbers of species that are able to coexist in a given location can be highly variable, shifting from more to fewer to more species again depending on the relative strengths of intra- versus interspecific interactions (Leibold, 1996; Liao et al., 2022). Likewise, as habitat is destroyed and habitat area decreases, losses (and gains) of species are not always monotonic, because previously dominant species become less dominant, allowing subordinate species to increase (Hastings, 1980; Nee & May, 1992; Tilman et al., 1997; Zhang et al., 2023). Such variability in the numbers of coexisting species along smooth

environmental gradients can create complex expectations for biodiversity responses.

Here, we illustrate the complex nature by which species diversity is expected to respond to the separate and interactive effects of three main drivers of biodiversity—habitat size, resource productivity, and disturbance—using a simple, but comprehensive theoretical model for multispecies communities based on the competition–colonization (C–C) trade-off (illustrated in Figure 1). The C–C framework has been used to make a number of predictions regarding how biodiversity should vary through time and space (Guo, Zhao, et al., 2023; Liao et al., 2022; Rybicki et al., 2020; Tilman, 1994; Tilman et al., 1994; Zhang et al., 2023). While by no means the only model that is able to explain such complex dynamics, we use it to examine the separate and interactive effects of these drivers on patterns of diversity in multispecies systems. We demonstrate a C–C trade-off mechanism by which these drivers can lead

to complex nonlinear, zig-zag responses in biodiversity. In addition, we find strong interactions between these drivers, which can cause the patterns of SAR, PDR, and DDR to shift, and even alter the general patterns. The combination of complex zig-zag responses and the strong interaction between drivers can help explain the mixed findings emerging from empirical studies.

METHODS

Competition–colonization modeling framework

We present a habitat with size S , representing the fraction of the total number of sites available for species colonization. Each site can only accommodate one individual of one species (illustrated in Figure 1). Thus, the

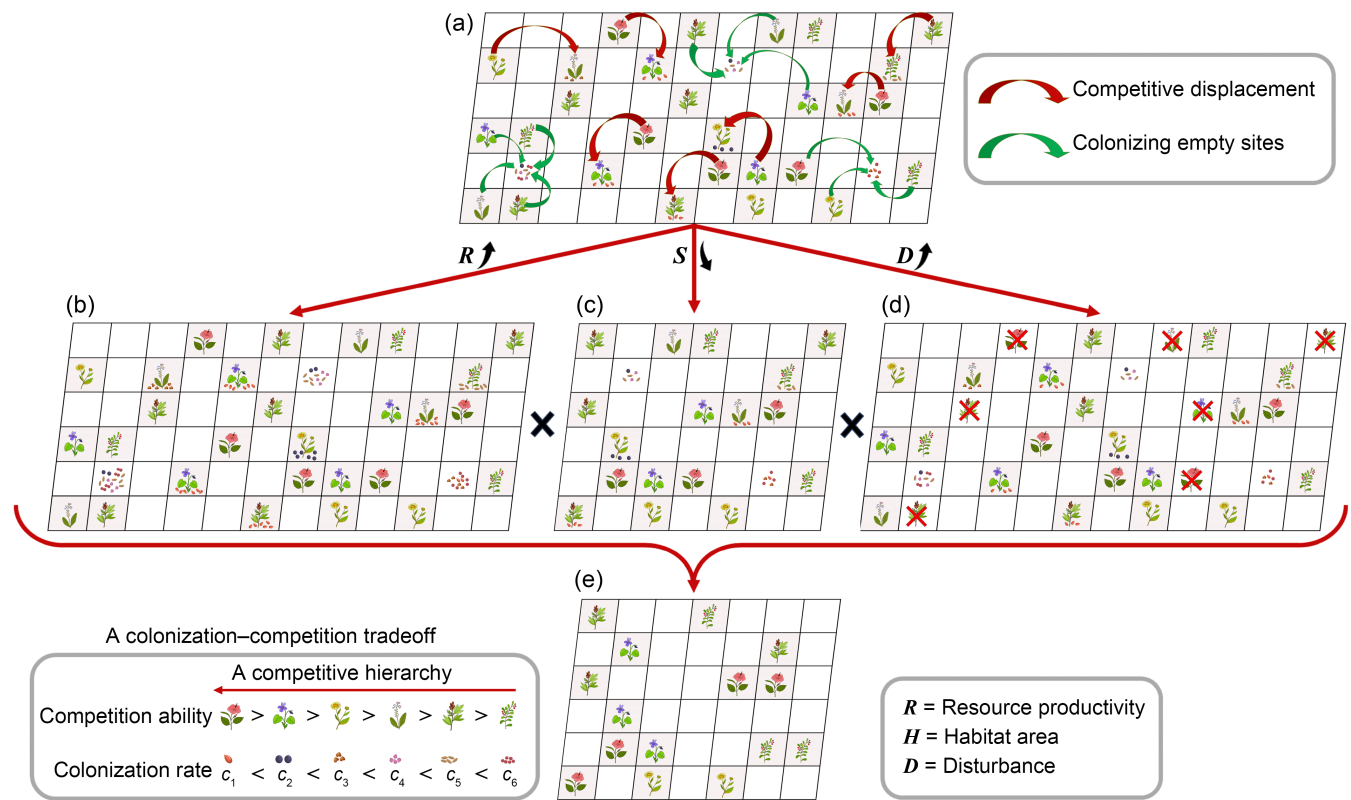


FIGURE 1 Illustration of the colonization–competition (C–C) trade-off model in a multispecies ($n = 6$ species) system subject to multiple environmental drivers, including habitat size (S), resource productivity (R), and disturbance (D). Panel (a): initial species diversity pattern, containing two potential processes: superior competitors displacing inferior competitors via propagules (red arrows), and species colonizing empty sites via propagules (green arrows). Panel (b): increasing resource productivity (R) is assumed to enhance the colonization rates of all species (i.e., increasing the amount of propagules, such as seeds). Panel (c): reducing habitat size (S) by directly removing sites from the initial habitat in panel (a) (i.e., habitat loss). Panel (d): stochastic disturbance resulting in species mortality randomly across the habitat (red cross). Panel (e): biodiversity pattern as the product of interactions between these three drivers (represented by bold black cross). To establish the C–C trade-off, we assume a competitive hierarchy by ranking the species from the best competitor (species 1) to the poorest (species 6), while setting species colonization rates as $c_1 < c_2 < c_3 < \dots < c_6$ (represented by the amount of propagules). All icons were obtained from <https://www.ztupic.com/> and are in the public domain.

population size of a species can be measured in terms of the fraction of sites that a species occupies (site occupancy), and population growth depends on the colonization–mortality dynamics. Under the simplifying assumption of the classic C–C model (Tilman, 1994; Tilman et al., 1994), coexistence between competitor species in a site is impossible on the timescale of the model; thus, competition leads to the displacement of a resident species by a superior competitor (*competitive displacement*). The probability of competitive displacement is determined by the relative competition strength (H_{ij}) of the species involved (Grilli et al., 2017; Li et al., 2020; Liao et al., 2022). Based on previous models (Guo, Barabás, et al., 2023; Guo, Zhao, et al., 2023; Li et al., 2020; Liao et al., 2022; Zhang et al., 2023), we can write the site-occupancy dynamics (p_i) of species i in an n -species system by incorporating the three environmental factors of interest: habitat size (S), resource productivity (R), and disturbance $f(t, D, T)$.

$$\frac{dp_i}{dt} = \underbrace{c_i R p_i \left(S - \sum_{j=1}^n p_j \right)}_{\text{Colonization}} + \underbrace{R \sum_{j=1}^n (c_i p_i H_{ij} p_j - c_j p_j H_{ji} p_i)}_{\text{Competitive displacement}} - \underbrace{p_i f(t, D, T) - m_i p_i}_{\text{Disturbance Mortality}} \quad (1)$$

Species site-occupancy dynamics are subject to the *colonization–competition–disturbance–mortality* processes, with c_i representing the colonization rate of species i and m_i represents its mortality rate. Following previous work (Kondoh, 2001; Svensson et al., 2012; Worm et al., 2002), we assume that increasing resource productivity (R) can enhance the colonization rate of all species by scaling them with a unitless factor R .

In Equation (1), the *colonization* term characterizes the rate at which species are able to establish on empty sites, and the *competitive displacement* term is the sum of the net result of pairwise competition events, both depending on the colonization pressure (e.g., $c_i R p_i$) exerted by these species. Specifically, *competitive displacement* occurs when colonizers (e.g., propagules) from one species ($c_i R p_i$ or $c_j R p_j$) arrive at a site occupied by another species and displace it. Both coefficients H_{ij} and H_{ji} , which are encoded in a competitive matrix \mathbf{H} , represent the independent probabilities that an individual of species i displaces species j and that species j displaces species i , respectively. These probabilities can be used to describe complex competitive structures, such as strict hierarchical competition by setting $H_{ij} = 1$ if $i < j$ and 0 otherwise (Tilman, 1994; Tilman et al., 1994), and intransitive

competition by reshuffling the hierarchical matrix \mathbf{H} (Rojas–Echenique & Allesina, 2011). The *disturbance* term in Equation (1) contains a forcing function $f(t, D, T) > 0$, ensuring that a fraction D ($0 < D < 1$) of each species is removed within each period T .

Model analysis

As shown in Equation (1), the *per capita* growth rate of species i can be rearranged as

$$r_i = \frac{1}{p_i} \frac{dp_i}{dt} = \underbrace{c_i R S - m_i - f(t, D, T)}_{b_i} + R \sum_{j=1}^n \underbrace{(c_i H_{ij} - c_j H_{ji} - c_i)}_{A_{ij}} p_j, \quad (2)$$

where b_i is the effective intrinsic growth rate of species i , and A_{ij} is the effective interaction coefficient in matrix \mathbf{A} (i.e., the effects of intra- and interspecific competition). Equation (2) for the *per capita* growth rate ($r_i = \frac{1}{p_i} \frac{dp_i}{dt}$) of species i falls in the category of linear and additive models, where the time-averaged model's behavior matches the long-term dynamics of the original one (Barabás et al., 2018; Chesson, 1994; Liao et al., 2022). Thus, the precise form of disturbance $f(t, D, T)$ does not matter, with only its time average being relevant for the long-term dynamics. Because we assume that the disturbance removes a fraction $D \in (0, 1)$ of each species (i.e., p_i drops to $(1 - D) \times p_i$) during every period T , we set this average to be

$$\bar{f}(t, D, T) = -\frac{1}{T} \log(1 - D) > 0, \quad (3)$$

which gives the same long-time average result as a model with periodic disturbance (Liao et al., 2022). To explain this, we calculate how much mortality a rate of $\bar{f}(t, D, T)$ causes within one period T . Integrating $\frac{dp_i}{dt} = -p_i \times \bar{f}(t, D, T) = -p_i \times \left[-\frac{1}{T} \log(1 - D) \right]$ over time, we derive $p_i(t) = p_i(0) \times \exp\left[\log(1 - D)^{t/T} \right]$, or equivalently, $p_i(t) = p_i(0) \times (1 - D)^{t/T}$. This gives $p_i(T) = p_i(0) \times (1 - D)$ for $t = T$, satisfying the assumption that p_i drops to $p_i(1 - D)$ during each period T . In fact, our results will hold for any specific form of $f(t, D, T)$ satisfying this criterion. Furthermore, the effects of a disturbance with extent D and periodicity T are equivalent to the effects of another disturbance with extent $D' = 1 - (1 - D)^{1/T}$ and periodicity $T' = 1$, derived from

$-\frac{1}{T} \log(1 - D) = -\frac{1}{T'} \log(1 - D')$ by setting $T' = 1$. Thus, here we only vary D while keeping $T = 1$ throughout, which is sufficient for achieving a full understanding of the impact of disturbance (similar to Kondoh, 2001; Svensson et al., 2012; Worm et al., 2002).

The *per capita* growth rate $r_i = \frac{1}{p_i} \frac{dp_i}{dt}$ of species i has the Lotka–Volterra form $r_i = b_i + R \sum_{j=1}^n A_{ij} p_j$, which is linear with respect to p_j . This linearity allows one to take the time average of the *per capita* growth rate directly:

$$\bar{r}_i = \bar{b}_i + R \sum_{j=1}^n A_{ij} \bar{p}_j, \tag{4}$$

where \bar{p}_j represents time-averaged site occupancy of species j . Thus, Equation (4) has at most one fixed point, where all species populations p_i^* are positive (i.e., a coexistence steady state). At this steady state ($\bar{r}_i = 0$), we can express the long-term average site occupancy of species i explicitly by inverting the matrix \mathbf{A} :

$$\bar{p}_i^* = - \sum_{j=1}^n (\mathbf{A}^{-1})_{ij} \times \left(\frac{\bar{b}_j}{R} \right), \tag{5}$$

where $\bar{b}_j = c_j R S - m_j + \log(1 - D)$ is the effective intrinsic growth rate, and $(\mathbf{A}^{-1})_{ij}$ is the (i, j) th entry of the inverse of the effective interaction matrix \mathbf{A} , with $A_{ij} = c_i H_{ij} - c_j H_{ji} - c_i$. If the competitive matrix \mathbf{H} is fully hierarchical ($H_{ij} = 1$ if $i < j$ and 0 otherwise), the feasible equilibrium point where the most species survive is stable (see stability analysis in Appendix S1: Section S1).

Numerical analysis

We use the modeling framework above to analyze how habitat size (S), resource productivity (R), and disturbance extent (D) interact to influence biodiversity in an n -species system at steady state (illustrated in Figure 1). We first 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 $c_1 < c_2 < c_3 < \dots < c_n$ in order to establish the possibility of C–C trade-offs (Tilman, 1994; Tilman et al., 1994). Using stability analysis of feasible equilibria (Appendix S1: Section S1.1), we find that 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 in a competitive hierarchy (Appendix S1: Section S1.2).

Regardless of dynamical behavior, initial species abundances do not affect system steady state, thus they were randomly generated ($0 < p_i < 1$), with the sum equal to habitat size ($\sum_{i=1}^n p_i = S$). To determine species abundances at steady state for a wide range of parameters, we applied numerical methods (via ODE45 in Matlab R2016a version; see code in Liao & Zhang, 2023) to simulate each case. Based on preliminary trials, we found that five million time units were sufficient for all cases to achieve steady state. Therefore, we ran each case for five million time units, and then kept it running for an additional five thousand time units, which we used to estimate the time-averaged population size for each species at steady state. We deemed a species extinct if its population size at steady state dropped below 10^{-6} , as such populations were typically eliminated by environmental fluctuations. We measured biodiversity using two metrics from two ends of the Hill (1973) number continuum that differentially weigh common and rare species (Chao et al., 2014): species richness (i.e., the number of species), which weighs common and rare species equally, and the inverse Simpson index ($1/\sum q_i^2$, with $q_i = p_i/\sum p_j$ being the relative abundance of species i), which places greater weight on more common species.

RESULTS

To illustrate key behavior and results from the C–C trade-off model, we first implement a numerical simulation to explore the separate effects of S , R , and D in a simple multispecies community ($n = 6$ in Figure 2; $n = 3$ in Appendix S2: Figure S1). We show the results from two cases, which are set by evenly spacing species colonization rates in different ranges. In the first case (Case 1), we allow all species to coexist in an intact habitat (i.e., $R = S = 1$ and $D = 0$; Figure 2a–c) to illustrate whether species diversity responds to habitat size in a monotonic fashion. In the second case (Case 2), we set parameters such that only some species can coexist in an intact habitat as a result of competitive exclusion (Figure 2g–i), to illustrate how the response of biodiversity to resource productivity or disturbance can be hump-shaped (Connell, 1978; Grime, 1973). We can see that there are general characteristic patterns of increasing diversity with increasing S and R , and decreasing diversity with increasing D in Case 1 (Figure 2a–c), but clear hump-shaped patterns for S , R , and D in Case 2 (Figure 2g–i). These overall patterns were more pronounced for species richness than the inverse Simpson index, which accounts for species relative abundances. Importantly, however, there were abrupt transitions along the gradient of each driver, which we here refer to as zig-zag responses across environmental gradients. These zig-zag patterns, where both species richness and

the inverse Simpson index have multiple peaks and troughs, create a considerable amount of variation in diversity responses to each driver (Figure 2a–c,g–i).

When we compared six-species and three-species communities (Figure 2 vs. Appendix S2: Figure S1), we found more biodiversity peaks in the species-rich system.

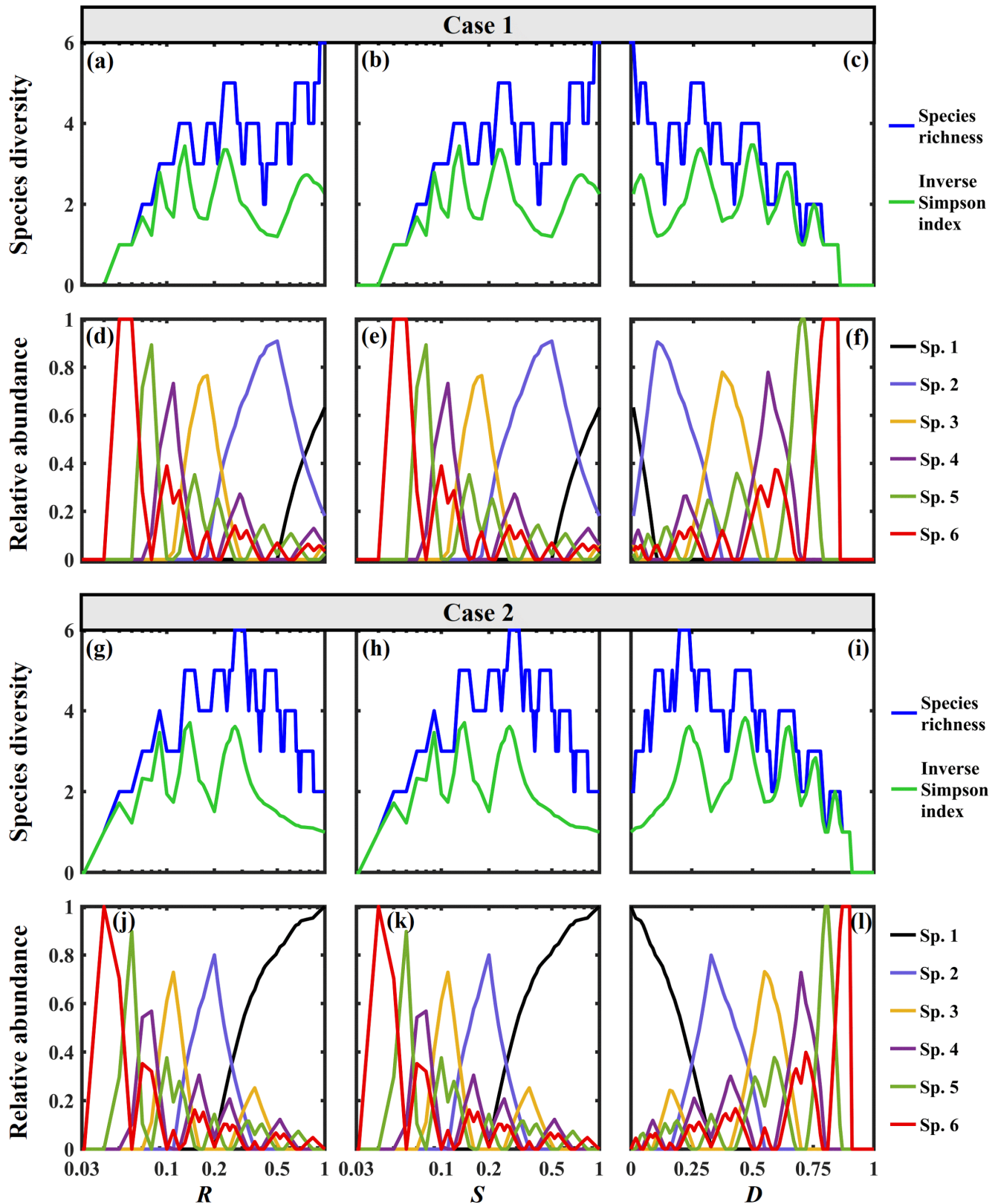


FIGURE 2 Legend on next page.

The zig-zag response in biodiversity emerges from patterns in how species relative abundances in the community change along gradients of each driver (Figure 2d–f,j–l; Appendix S2: Figure S1). The points on the environmental gradient at which a species can enter or leave the system are “turning points.” At these points, trends in relative abundance reverse, where species in decline switch to increase in relative abundance and *vice versa*. These turning points arise from the interaction between environmental drivers and C–C trade-offs (Figure 2d–f,j–l). For example, in Case 1 (Figure 2d–f), we find a monotonic decline in the abundance of the most superior competitor (species 1 with the lowest colonization rate) in all scenarios where the environment is diminished, either by decreasing the habitat size (S) or resource productivity (R), or by increasing disturbance extent (D). As a direct result of the decline of Species 1, the second most competitive species (with the second worst colonization ability—Species 2) is released from competition pressure and increases, which cascades to affect Species 3 negatively, affect Species 4 positively, and so on. As a result, this “zig-zag” pattern in species abundances with environmental deterioration naturally translates to a zig-zag diversity profile along these gradients.

Next, we illustrate how these three drivers interact by showing how each pairwise combination of S , R , and D influences patterns of species richness and the inverse Simpson index (Figure 3; Appendix S2: Figure S2). In both cases, we observe multiple bands of high and low species diversity that emerge naturally along environmental gradients. As these bands form across all drivers, they can shape a sequence of multiple peaks and troughs in both measures of species diversity along gradients of each driver, as displayed in both Figure 2 and Appendix S2: Figure S1.

Beyond the illustrative scenario with a small number of species ($n = 3$ or 6), we extend our analysis to a larger community with species pool $n = 100$ to explore how each pair of drivers interact to affect biodiversity patterns (Figure 4). We find the same zig-zag pattern in biodiversity, with bands of lower and higher diversity alternating frequently across all environmental drivers (Figure 4). As such, we can simplify our analysis by considering how

species diversity varies along each environmental driver. We again find that both measures of diversity fluctuate significantly in a zig-zag pattern as each driver varies (Figure 5 and Appendix S2: Figure S3). Similarly, these zig-zags in diversity result from a checkerboard pattern in species relative abundances along the environmental gradient (i.e., the alternating pattern of species entering or leaving the system in Appendix S2: Figure S4d–f,j–l). To further explain this, we provide a mathematical proof in terms of how the equilibrium average site occupancies \bar{p}_i^* respond to multiple drivers (Appendix S1: Section S2). Again the overall patterns of diversity in response to each driver are either monotonic or unimodal in both cases (Figure 5; Appendix S2: Figures S3 and S4). This is because in Case 1 where all species co-occur in an intact habitat, environmental deterioration (i.e., decreasing R or S , or increasing D) leads to species extinctions along a sequence from the best competitor to the poorest (Appendix S2: Figure S4d–f). Alternatively, in Case 2 where the best competitor dominates the intact habitat, its decline in relative abundance with environmental deterioration allows poor competitors (with higher colonization rates) to enter the system sequentially. However, as the environment deteriorates further, species extinction again follows a sequence from the best competitor to the poorest (Appendix S2: Figure S4j–l). We further find strong interactions between these drivers, which can create variable patterns of SAR, PDR, and DDR, even fundamentally altering the general characteristic patterns in biodiversity (Figure 5; Appendix S2: Figure S3). For example, in Case 2 (Figure 5g–l Appendix S2: Figure S3g–l), the overall patterns in SAR, PDR, and DDR are unimodal in benign environments (i.e., large habitat size, little disturbance or/and high productivity), but they can shift to become monotonic when the environment is diminished (e.g., reducing habitat size or productivity, or/and increasing disturbance).

Importantly, when we weaken (Appendix S2: Figure S5) or even violate the strict competitive hierarchy (Appendix S2: Figures S6 and S7), we find that such zig-zag responses of biodiversity to gradients of multiple drivers are robust (albeit somewhat weaker). For instance, we simulate intransitive competition with different levels

FIGURE 2 Separate effects of habitat size (S), resource productivity (R), and disturbance extent (D) on species diversity (a–c and g–i) and their relative abundances (d–f and j–l) in a simple multispecies community ($n = 6$), with a strict competitive hierarchy by ranking the species from the best competitor (species 1) to the poorest (species 6). Note that the x -axes of S and R are not evenly scaled in order to make the zig-zag pattern at $S < 0.5$ and $R < 0.5$ more distinguishable. Species diversity is characterized by both species richness and the inverse Simpson index. Species colonization rates (c_i) are evenly spaced in increasing order in both ranges: (Case 1) $c_i \in E[0.2, 2]$ with all species coexisting in an intact habitat (i.e., $R = S = 1$ and $D = 0$); and (Case 2) $c_i \in E[0.5, 2.5]$ with species competitive exclusion occurring in an intact habitat. Panels (a, d, g, and j): $S = 1$ and $D = 0$; panels (b, e, h, and k): $R = 1$ & $D = 0$; and panels (c, f, i, and l): $R = S = 1$. Others: species mortality rates $m_i = 0.1$.

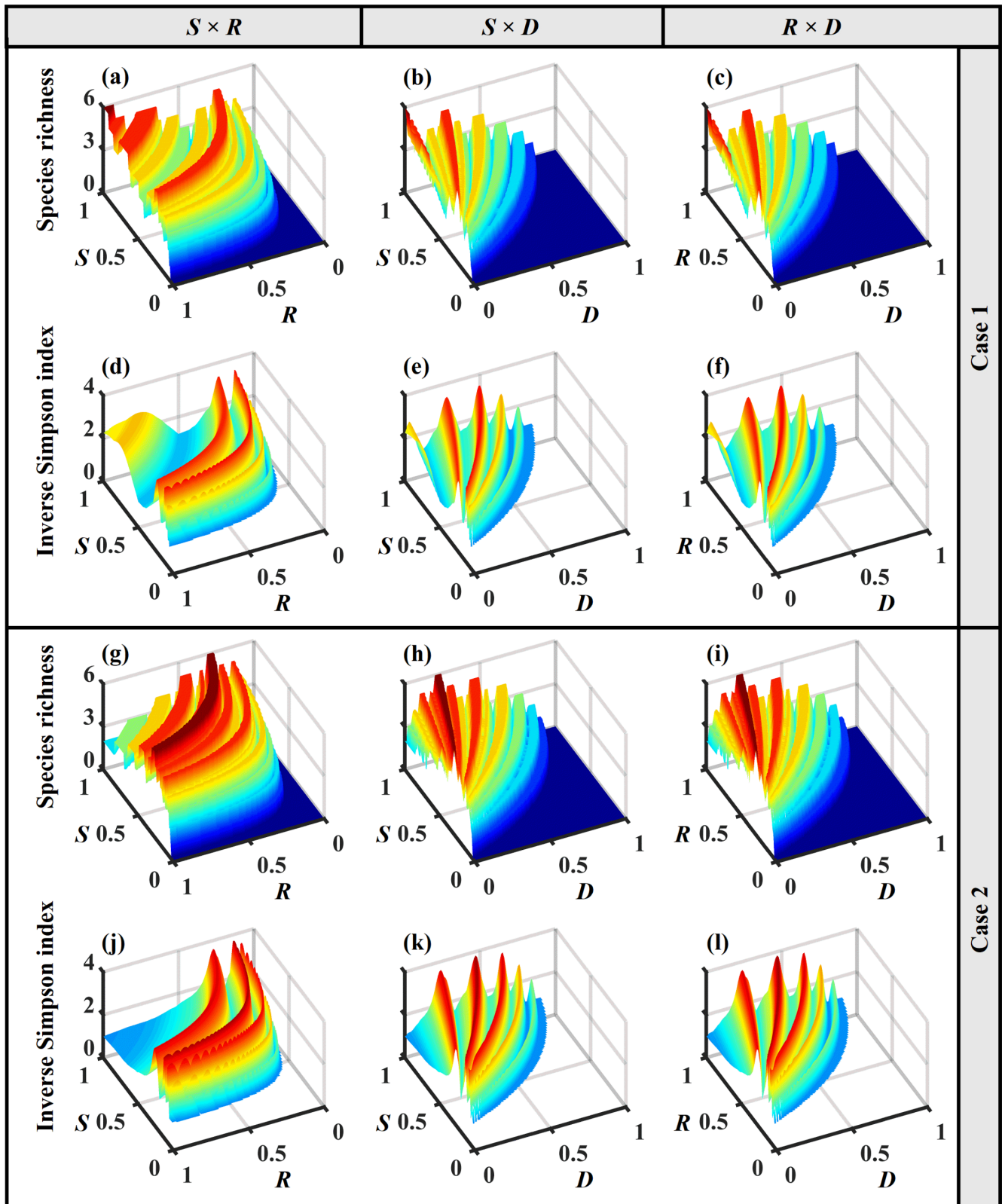


FIGURE 3 Interactive effects of habitat size (S), resource productivity (R), and disturbance extent (D) on biodiversity, characterized by species richness and the inverse Simpson index. Panels (a, d, g, and j): $D = 0$; panels (b, e, h, and k): $R = 1$; and panels (c, f, i, and l): $S = 1$. Other parameter settings are the same as in Figure 2.

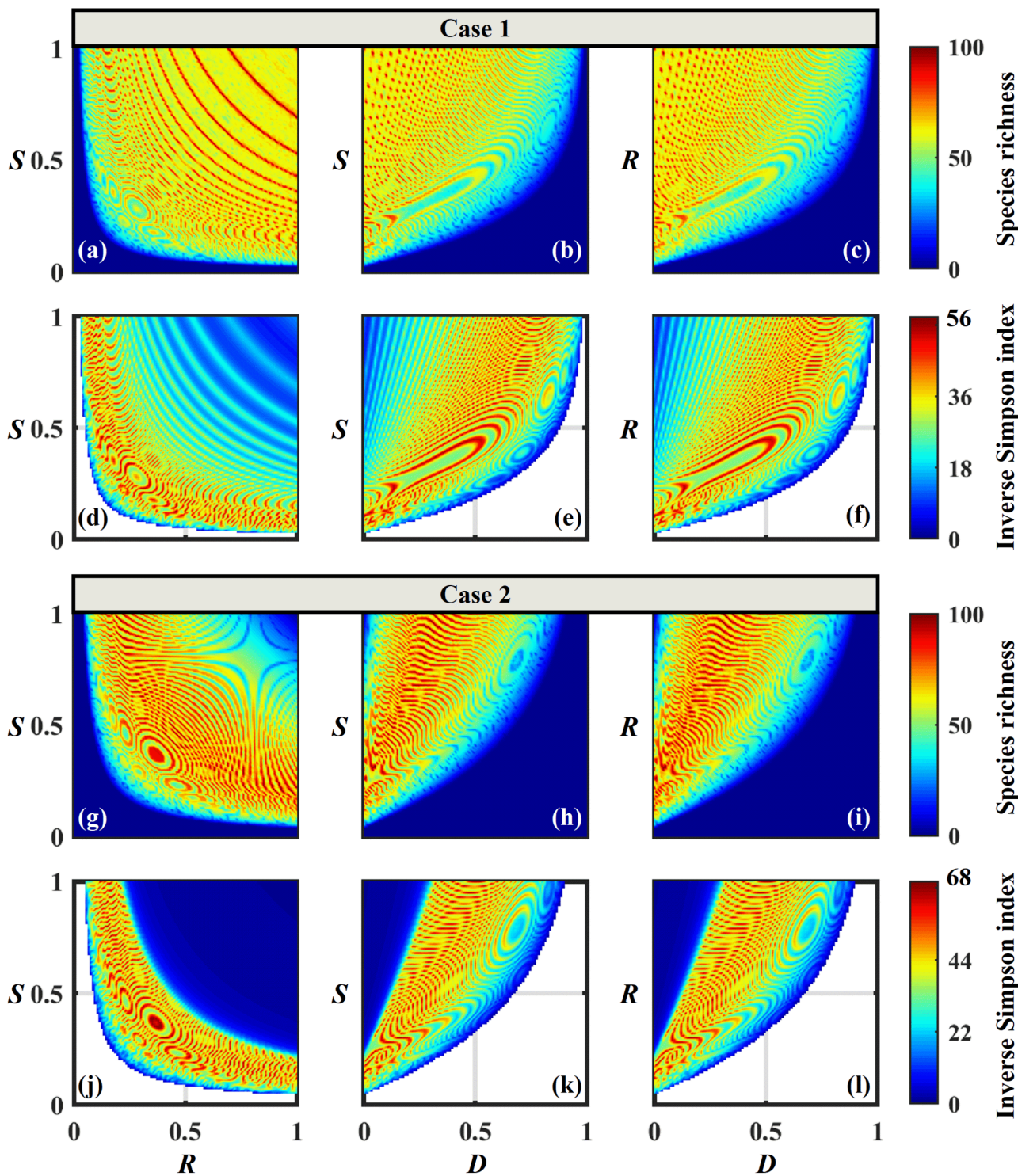


FIGURE 4 Interactive effects of habitat size (S), resource productivity (R), and disturbance extent (D) on biodiversity in a large initial community ($n = 100$), with a strict competitive hierarchy by ranking the species from the best competitor (species 1) to the poorest (species 100). Species diversity is characterized using species richness and the inverse Simpson index. Species colonization rates (c_i) are evenly spaced in increasing order in both ranges: panels (a–f) $c_i \in E[0.12, 4.575]$ in Case 1 where all species can coexist in an intact habitat (i.e., $R = S = 1$ and $D = 0$); and panels (g–l) $c_i \in E[0.5, 2.5]$ in Case 2, with species competitive exclusion occurring in an intact habitat. Panels (a, d, g, and j): $D = 0$, panels (b, e, h, and k): $R = 1$, and panels (e, f, i, and l): $S = 1$. Other parameters: $m_i = 0.1$.

of relative intransitivity ($RI = 0.5$ and 1 in Appendix S2: Figures S6 and S7; see the generation method in Rojas-Echenique & Allesina, 2011), and find similar,

although less pronounced, zig-zag patterns in biodiversity. This is because, instead of a global C–C trade-off, there only exist local C–C trade-offs involving different subsets

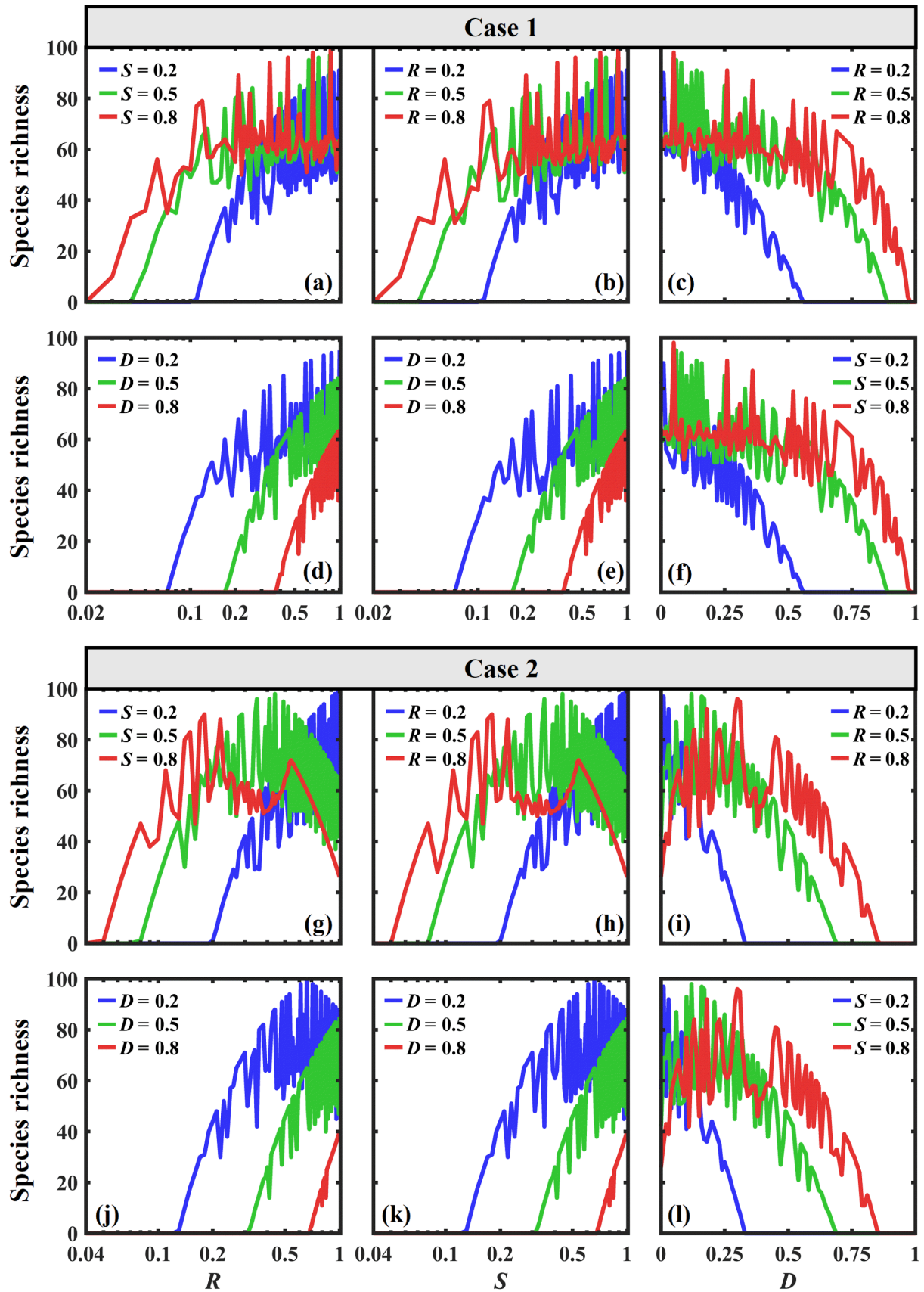


FIGURE 5 Separate effects of habitat size (S), resource productivity (R), and disturbance extent (D) on species richness in a large initial community ($n = 100$), by varying other drivers at different levels (S, R or $D = 0.2, 0.5$, and 0.8). Panels (a, b, g, and h): $D = 0$, panels (c, d, i, and j): $S = 1$, and panels (e, f, k, and l): $R = 1$. Other parameter settings are the same as in Figure 4.

of the species in the system. Likewise, we continue to observe biodiversity zig-zags in response to multiple drivers for communities with irregularly spaced colonization rates (e.g., uniformly sampled in Appendix S2: Figures S8–S10 and geometrically spaced in Appendix S2: Figures S11 and S12), albeit with fewer peaks in biodiversity. However, when species colonization rates are set as a geometric series with $c_i = c_1 \times q^{i-1}$ (common ratio $q > 1$) in a strict C–C trade-off, the zig-zag pattern disappears and becomes more of a “stairstep” for species richness against each driver (Appendix S2: Figures S11 and S12). More specifically, when $q \geq \frac{c_1}{m}$ ($c_1 > m$), all species can co-occur in a fully intact habitat (i.e., $S = R = 1$ & $D = 0$), thereby shaping the stepwise decline in species richness with environmental deterioration (Appendix S2: Figure S11). If $1 < q < \frac{c_1}{m}$, species competitive exclusion occurs in the intact habitat, forming the unimodal stairstep pattern in species richness (Appendix S2: Figure S12). Yet, the zig-zag pattern still occurs for the inverse Simpson index because of its sensitivity to changes in species relative abundances (Appendix S2: Figures S11 and S12). To further demonstrate the generality of our outcome, we explore several other scenarios. For example, we examine when resource productivity is assumed to only affect colonization or competition (Appendix S2: Figures S13 and S14), as well as when disturbance is represented in a simpler form $f(t, D, T) = D$ (Appendix S2: Figure S15), and influences colonization, competition, or both simultaneously (Appendix S2: Figures S16–S18). In each scenario, we find that the zig-zag pattern in biodiversity emerges as a result of the C–C trade-off among species.

DISCUSSION

Using an extended C–C trade-off model, we here demonstrate two key expectations for the separate and interactive roles of three critical biodiversity drivers, habitat size, resource productivity, and disturbance. First, we find that complex zig-zag patterns in biodiversity emerge naturally along gradients of each driver. Second, these drivers interact to influence the expected patterns along gradients. Even though we often search for prevailing theoretical expectations and empirical patterns, for example, a monotonic positive SAR, or unimodal PDR and DDR, these expectations fail to capture the full complexity of these relationships. As a result, it is not surprising, and perhaps even expected, that we would find considerable variation in biodiversity responses to multiple drivers within and among empirical studies (Cusens et al., 2012; Fahrig, 2017; He et al., 2024; Mackey & Currie, 2001; Mittelbach

et al., 2001; Svensson et al., 2012; Viljur et al., 2022; Whittaker, 2010). Although our results indicate that SAR, DDR, and PDR patterns can be highly variable, it is also not surprising that certain types of patterns are more often observed in natural communities. For example, superior competitors are favored in less disturbed or highly productive environments, while superior colonizers tend to dominate in highly disturbed or low productive ecosystems (Kondoh, 2001; Roxburgh et al., 2004; Worm et al., 2002), leading to the observation that the highest levels of biodiversity often occur at intermediate levels of disturbance or productivity (Connell, 1978; Fraser et al., 2015; Grime, 1973; Mittelbach et al., 2001; Tilman, 1993; Worm et al., 2002). In such cases, when these data are fitted with a quadratic function, the zig-zag patterns we predicted would simply be viewed as statistical noise around this relationship, thereby shaping a typical unimodal DDR and PDR. Likewise, even though zig-zag patterns can emerge in SARs, we expect an overall positive relationship in most empirical studies (Chase et al., 2020; He & Hubbell, 2011). This is because if all species co-occur in an intact habitat, species extinctions with habitat loss will tend to follow a sequence from the best competitor to the weakest, albeit with substantial variation. By fitting such SARs with nondecreasing functions and treating the substantial variation in species richness as statistical noise, the general increasing SAR will be most prevalent.

The zig-zag response of biodiversity to gradients of the three environmental drivers that we observed is quite robust and generic, only requiring the assumption that there is a trade-off between competitive ability and colonization rate. This assumption is necessary for species to coexist, but also sets the stage for the zig-zag responses. In large, productive, and undisturbed habitats, the superior competitor dominates the system and exists alone. However, as ecosystems become smaller, have lower productivity, and/or suffer more disturbance, the abundance of this superior competitor is diminished because of its low colonization rate. This leaves more space available for inferior competitors with high colonization rates. Which, and how many, of these species can coexist is mediated by the interaction between C–C trade-offs and these drivers. Essentially, this interaction can shape an asymmetric control mechanism, which can facilitate different subsets of species to coexist along environmental gradients. Specifically, the species directly adjacent to the superior competitor in the competitive ranking will be suppressed the most, because it is compensated the least from its advantage in colonization rate. This, in turn, benefits the species one step further down the competitive ranking, causing the peaks in the relative abundance of adjacent species to alternate. As environmental conditions deteriorate, this eventually leads to the extinction of

the most dominant competitor and the emergence of a new dominant species. Repeating this process with environmental deterioration would therefore create a zig-zag pattern in species diversity along the environmental gradient. Importantly, however, the magnitude of the zig-zag response becomes weaker at both lower and higher levels of these drivers. As most species in the system either are competitively excluded in benign environments (large habitat area, high resource productivity or low disturbance) or go demographically extinct in harsh environments (low resource or habitat availability, or high disturbance), low-diversity communities at the extremes will have weaker peaks in their zig-zag responses.

While the zig-zag pattern we have observed here emerged because of the strict C–C trade-off we imposed on the system, similar zig-zag responses along environmental gradients can be expected in other theoretical contexts (Banitz et al., 2008; Johst & Huth, 2005; Leibold, 1996; Svensson et al., 2012). For instance, Leibold (1996) qualitatively analyzed a model of species interactions involving the overall trade-off between resource exploitation ability (a bottom-up effect) and susceptibility to a predator (a top-down effect) and implied a zig-zag response in species diversity along the resource productivity gradient. Our results generalize this expectation by systematically exploring multiple environmental variables and their interactions in a C–C trade-off context. However, the shape and emergence of the zig-zag patterns themselves can vary. Even in the same theoretical context, previous analyses of similar C–C trade-off models have not observed such zig-zag patterns (e.g., Kondoh, 2001; Tilman et al., 1994, 1997). This is because these analyses set variation in species colonization rates as a geometric series with a fixed common ratio, where they can shape a perfectly synchronized zig-zag pattern in species relative abundances along the environmental gradient. In addition, there are approximately half of the species at peaks while the other half at troughs at each turning point, associated with species just entering (from the best colonizer to the poorest) or leaving (from the best competitor to the weakest) the system sequentially with environmental deterioration (see Appendix S2: Figures S11 and S12). In such a case, a staircase pattern in raw species richness is expected due to a sharp change in the trajectories of species relative abundances against each driver. Interestingly, however, even when there is no zig-zag for species richness, we still observe a zig-zag response in the inverse Simpson index, which integrates aspects of species relative abundances (Appendix S2: Figures S11 and S12). In fact, the specific geometric constraint placed on earlier analyses is neither realistic nor necessary, as there are many other settings for species colonization rates that enable all species to

coexist in an intact habitat (e.g., evenly spaced in Case 1 of Figures 2–4). If we adopt other parameter settings, for example, species colonization rates are evenly spaced or uniformly sampled, or a strict competitive hierarchy is violated or reshuffled, and then such a perfect “synchrony” of the zig-zag pattern in species relative abundances would be perturbed, thereby yielding the complex response in species richness we observed.

Despite their emergence from theory, empirical evidence for zig-zag patterns in biodiversity along environmental gradients has been elusive for several reasons. First, experimental studies often tried to take several environmental gradients or a small range of environmental regimes as representative of the effect of the full range, therefore neglecting regimes that could drive the emergence of more complex community dynamics. Second, even when a full range of environmental regimes was considered, experiments may have been designed with insufficient statistical power to detect zig-zag patterns, as it is difficult to discern noise from more directed zig-zag patterns in empirical studies. Finally, some field experiments, typically conducted in terrestrial plant communities within a short term, cannot observe competitive exclusion or stable species coexistence (Shea et al., 2004). Consequently, these experiments are not suitable to establish the complete linkage between environmental drivers and C–C trade-offs. Nevertheless, some empirical studies have observed multiple diversity peaks in response to environmental drivers. For example, responses to disturbance in aquatic ecosystems (Cadotte, 2007; Gibbons et al., 2016; Hall et al., 2012; Lenz et al., 2004) suggest that long-term experiments along high-resolution environmental gradients could capture zig-zag patterns in biodiversity.

In addition to zig-zag patterns of biodiversity and species composition along gradients of environmental drivers, another reason why we are unlikely to expect simple general patterns in SAR, PDR, or DDR is because of the strong interactions between these drivers (see also Kondoh, 2001). In our model, we find that these interactions can cause the SAR, PDR, and DDR to shift, and even fundamentally alter the general patterns in biodiversity, as sometimes observed empirically (Death & Zimmermann, 2005; Dodson et al., 2000; Kneitel & Chase, 2004; Ónodi et al., 2021; Proulx & Mazumder, 1998; Scholes et al., 2005). For example, Ónodi et al. (2021) observed that fire disturbance shifted the PDR from linearly increasing to unimodal in a long-term study in Hungarian grasslands, while Proulx and Mazmuder (Proulx & Mazmuder, 1998) found a general trend of the reversal of grazing impact on plant species richness in nutrient-poor versus nutrient-rich ecosystems. Furthermore, Dodson et al. (2000) observed that lake size can fundamentally alter the observed PDR of phytoplankton and fish.

The combination of complex zig-zag response of biodiversity to multiple environmental drivers, as well as the interactions among drivers, indicates that a change in perspective on expectations of biodiversity variation along ecological gradients is needed. We argue that the noisiness of biodiversity responses to environmental changes typically observed in empirical studies might not simply reflect sampling effects, measurement error, transient effects, or stochasticity. Instead, the noise arises deterministically from the underlying trade-off structure for species coexistence (in this case, C–C dynamics) in multispecies systems. This can also help explain why management actions sometimes intended to enhance biodiversity, including restoring habitats, reducing disturbance, or enriching resources, do not always have the intended outcome (Butchart et al., 2010). Thus, we advise caution when designing conservation strategies for biodiversity. Identification of the competitive structures, species demographic traits, and environmental characteristics from empirical data are essential precursors to setting conservation priorities in applied ecology. Furthermore, biodiversity is not necessarily a good measure of conservation success. Given the zig-zag relationship between biodiversity and multiple environmental drivers in a multispecies system, an observed increase in biodiversity would not necessarily indicate that the system would be able to tolerate more environmental deterioration. In fact, according to our model, a system that is near catastrophic collapse may experience sudden biodiversity increases in response to environmental change before any further habitat deterioration induces its actual decrease. This is conceptually analogous to a “hydra effect” (Hydra, refers to the mythical creature that grew more heads as each was chopped off by Hercules), whereby high rates of mortality can actually lead to greater population sizes (Abrams, 2009; Abrams & Matsuda, 2005). Thus, both biodiversity and system robustness to environmental alteration, instead of biodiversity alone, are required to evaluate conservation success.

AUTHOR CONTRIBUTIONS

Jinbao Liao conceived the study and wrote the first draft. Zeyu Zhang and Jinbao Liao built the model. Zeyu Zhang conducted model analysis and simulations. Zeyu Zhang and Jinbao Liao analyzed the results. Jonathan M. Chase and Daniel Bearup contributed substantially to revising and editing the draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No empirical data were collected for this study. Novel code (Liao & Zhang, 2023) is available on Zenodo: <https://doi.org/10.5281/zenodo.10131655>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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