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Complex non-monotonic responses of biodiversity to habitat destruction

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Abstract

It has typically been assumed that habitat destruction, characterized by habitat loss and fragmentation, has consistently negative effects on biodiversity. While numerous empirical studies have shown the detrimental effects of habitat loss, debate continues as to whether habitat fragmentation has universally negative effects. To explore the effects of habitat fragmentation, we develop a simple model for site-occupancy dynamics in fragmented landscapes. With the model, we demonstrate that a competition-colonization tradeoff can result in non-linear oscillatory responses in biodiversity to both habitat loss and fragmentation. However, the overall pattern of habitat loss reducing species richness is still established, in line with empirical observations. Interestingly, the existence of localized oscillations in biodiversity can explain the mixed responses of species richness to habitat fragmentation *per se* observed in nature, thereby reconciling the debate on the fragmentation-diversity relationship. Therefore, this study offers a parsimonious mechanistic explanation for empirically observed biodiversity patterns in response to habitat destruction.

Introduction

Understanding the effects of habitat destruction on biodiversity is a central issue in ecology and conservation (Tilman, 1994; Ehrlich, 1995; Tilman et al., 1994, 1997; Tilman & Kareiva, 1997; Neuhauser, 1998; Adler & Mosquera, 2000; Fahrig, 2001; Chase et al., 2020; Riva & Fahrig, 2023). According to previous work (Wilcox & Murphy, 1985; MacGarigal & Cushman, 2002; Fahrig, 2002, 2003; Hadley & Betts, 2016), habitat destruction consists of two main components: habitat loss and habitat fragmentation. The former is the reduction in the amount of available habitat, while the latter refers to the breaking apart and thus the change in the spatial arrangement of the remaining habitat. It is widely accepted that habitat loss has large, consistently negative effects on biodiversity (Chase et al., 2020), so ecologists who conceptualize and measure fragmentation as equivalent to habitat loss, typically extrapolate that habitat fragmentation *per se* also has large negative effects (Fahrig, 2003; Fletcher et al., 2018). However, recent research has challenged this extrapolation (Deane & He, 2018; Fahrig et al., 2019; Wintle et al., 2019; Arroyo-Rodriguez et al., 2020; Fahrig et al., 2022; Riva & Fahrig, 2023).

In a recent review of empirical studies, Fahrig (2017) has concluded that the effect of habitat fragmentation, independent of habitat loss, can be positive as well as negative, and even that positive effects outweigh negative ones (Fahrig et al., 2019; Riva & Fahrig, 2023). However, Fletcher et al. (2018) disputed this conclusion, arguing that the literature so far indicates generally negative ecological effects of habitat fragmentation *per se*. Thus, the precise form of the fragmentation-diversity relationship (FDR) remains a topic of debate (Fletcher et al., 2018; Fahrig et al., 2019). Instead of continuing this debate, many ecologists have advocated shifting the focus to elucidating the mechanisms responsible for those positive and negative fragmentation effects (Soranno et al., 2014; Prevedello et al., 2016; Fletcher et al., 2018; Fahrig et al., 2019).

Ecological theory has proposed a variety of mechanisms to explain the contrasting effects of fragmentation *per se* on biodiversity. For example, negative fragmentation effects are generally attributed to minimum patch size effects or negative edge effects, while positive fragmentation effects might result from increased functional connectivity, habitat heterogeneity, positive edge effects, refuge effects, landscape complementation, reduced competition and spreading of risk (Fahrig, 2003, 2017; Rybicki et al., 2020). However, most models based on these mechanisms are limited to describing only specific effects (but Ben-Hur & Kadmon, 2020; Rybicki et al., 2020). In particular, few studies have attempted to develop a holistic mechanistic mathematical model which can produce, and thus explain, both positive and negative responses to habitat fragmentation *per se*.

To explore the empirical observations on the relationship between habitat destruction and biodiversity (see meta-analyses in Chase et al., 2020; Riva & Fahrig, 2023), we develop a simple, spatially implicit framework for site-occupancy dynamics incorporating the separate effects of habitat loss and fragmentation. As suggested by Rybicki et al. (2020), this framework particularly considers the competition-colonization (C-C) tradeoff among species, which has been widely applied to diverse communities, such as grasses/vascular plants, forests (e.g., shrubs, herbs and ground cover plants), ant colonies, as well as insect and mammal communities (Yu & Wilson, 2001; Calcagno et al., 2006). With this model, we demonstrate that such a C-C tradeoff can produce non-linear, oscillatory responses in biodiversity along gradients of increasing habitat loss and fragmentation. This more complex potential response provides an explanation for variation in biodiversity responses found in recent empirical studies (Fahrig, 2017; Riva & Fahrig, 2023). Furthermore, we observe that the overall pattern remains a decline in biodiversity as levels of habitat destruction increase as is observed in nature (Chase et al., 2020).

Methods

Spatially implicit model for fragmented landscapes

In this section, we describe a model for site occupancy dynamics in a fragmented landscape. We begin by outlining a standard, spatially implicit, representation for a landscape subject to habitat loss and fragmentation. Then we formulate differential equations describing the mean-field behavior of a multispecies community on this landscape.

Following Hiebeler (2000), we represent a landscape subject to some level of habitat destruction by a lattice of square cells (i.e., habitat sites) which can take one of two types: suitable and unsuitable. Suitable sites can be colonized by at most one individual, while unsuitable sites cannot be colonized. This representation of a landscape allows habitat loss and spatial fragmentation to be characterized separately (Liao et al., 2013a, 2013b). Habitat loss is given by $1 - S$, where habitat availability

$S \in [0, 1]$ is the fraction of suitable sites in the landscape. Habitat fragmentation is given by $1 - Q$, where habitat connectivity $Q \in [0, 1]$ is the clumping degree of suitable sites in the landscape (Lloyd, 1967; Matsuda et al., 1992; Harada & Iwasa, 1994). According to the orthogonal neighbouring correlation based on von Neumann neighbourhood (Hiebeler, 2000), we have

$$2 - \frac{1}{S} < Q < 1. \qquad (1)$$

This means that Q cannot be too small if S is large. When $S<0.5$, this constraint vanishes. In particular, if suitable sites are randomly distributed across the landscape, $S = Q$ (i.e., randomly structured landscapes; Hiebeler, 2000). Note that this representation of a landscape is spatially implicit, as it does not describe the physical arrangement of habitat sites within the landscape.

Following Tilman's model (Tilman, 1994; Tilman et al., 1994, 1997), we describe mean-field site occupancy dynamics on this landscape in terms of *colonization-competition-mortality* processes. We assume that species can disperse randomly within habitat fragments (i.e., semi-local dispersal), while unsuitable sites block species dispersal between habitat fragments (e.g., physical barriers, such as roads, railways, traffic, fences, rivers, rock outcrops, etc.). This means that species dispersal across habitat fragments is impossible, but each habitat fragment always contains sufficient suitable sites to properly represent the global community state.

Due to the difficulty in constructing a closed system of equations for multispecies competition using pair approximation (Matsuda et al., 1992; Harada & Iwasa, 1994), we allow an increase in habitat connectivity to linearly increase all species' colonization rates by scaling them with a constant Q for model simplicity. This approach has been shown to be effective for approximating within-fragment dispersal in previous models (Liao et al., 2016, 2017a, 2017b, 2017c). We additionally perform spatially explicit simulations in fragmented landscapes (Appendix S1: Figure S1; Code in Liao, 2023), and obtain qualitatively similar biodiversity patterns as our dynamic model, confirming the validity of this dispersal approximation.

To describe competition between species, we make use of the assumption that species cannot coexist in a suitable site (Tilman, 1994). Thus competition can occur only through displacement of a resident by a superior competitor (*competitive displacement*). We further assume that colonization rate and competitive ability are subject to a tradeoff (C-C tradeoff; Tilman et al., 1994, 1997).

Based on these assumptions, we obtain the following description of the *colonization-competition-mortality* processes of a species i in an n-species community

$$\frac{dp_i}{dt} = \underbrace{c_i Q p_i\left(S - \sum_{j=1}^{n} p_j\right)}_{Colonization} + \underbrace{Q\sum_{j=1}^{n}\left(c_i p_i H_{ij} p_j - c_j p_j H_{ji} p_i\right)}_{Competition} \underbrace{- m_i p_i}_{Mortality} \ . \qquad (2)$$

The fraction of sites occupied by species i, and its colonization and mortality rates are given by p_i, c_i and m_i, respectively. The relative competition strength of species i compared to species j is H_{ij}, giving the probability that a colonizer of species i displaces a resident of species j from a site. The *mortality* term is straightforward: individuals are assumed to die with a rate m_i, thus the overall population loss for species i is given by $m_i p_i$.

The *colonization* term describes the rate at which species i can occupy empty suitable sites. The total number of colonizers (e.g., propagules) produced by species i is proportional to its population size ($c_i p_i$). The expected number of empty sites colonized by these colonizers is obtained by multiplying the fraction of empty suitable sites in the landscape ($S - \sum_{j=1}^{n} p_j$) and habitat connectivity Q. Here Q represents our assumption that unsuitable sites can block species dispersal and thus reduce the effective colonization rate. If Q is close to 1, i.e., all suitable sites are clustered together to form a large habitat fragment, then colonizers have access to all empty suitable sites in the landscape and the effective colonization rate is close to c_i. If Q is very small (highly fragmented), then suitable sites are over-dispersed, i.e., most suitable sites are surrounded by unsuitable sites, which block species dispersal. In this case, the species will have a reduced effective colonization rate $Qc_i \ll c_i$, representing the effect of habitat fragmentation.

The *competition* term describes competitive displacement: colonizers from one species ($c_i p_i$ or $c_j p_j$) arrive at a site occupied by another species and displace it, with probabilities encoded in the competitive matrix $\boldsymbol{H}$. The net change in the population size of species i due to displacement competition with species j is given by $\left(c_i p_i H_{ij} p_j - c_j p_j H_{ji} p_i\right)$. Thus, the *competition* term is the sum of the net result of pairwise competition events modified by the effect of habitat fragmentation (Q). Note that H_{ij} and H_{ji}, the probabilities that a colonizer of species i displaces a resident of species j and *vice versa*, are independent from each other (Li et al., 2020; Liao et al., 2022), unlike the zero-sum game ($H_{ij} + H_{ji} = 1$; e.g., species competing for an empty site in Grilli et al., 2017). In fact, the classic C-C model (Tilman, 1994) is a special case of our model, as it can be derived in a strict competitive hierarchy (i.e., setting $H_{ij} = 1$ if $i < j$ and $H_{ij} = 0$ otherwise). Furthermore, the matrix $\boldsymbol{H}$ can be used to describe various competition structures, such as intransitive competition by perturbing the competitive hierarchy (Laird & Schamp, 2008; Rojas-Echenique & Allesina, 2011; Li et al., 2020).

Model analysis

The model developed above can be used to predict the composition of a community at steady state for a given level of habitat loss and fragmentation. We use this to analyze the effects of these factors on community diversity.

Similar to Liao et al. (2022), Equation (2) can be rearranged to obtain

$$\frac{dp_i}{dt} = p_i\left[\underbrace{c_iQS - m_i}_{b_i} + Q\sum_{j=1}^{n}\underbrace{\left(c_iH_{ij} - c_jH_{ji} - c_i\right)}_{A_{ij}}p_j\right] = p_i\left[b_i + Q\sum_{j=1}^{n}A_{ij}p_j\right]. \quad (3)$$

In this formulation, b_i is the effective intrinsic growth rate of species *i* in the absence of other species, while A_{ij} is the effective interaction coefficient (i.e., the effects of intra- and inter-specific competition). The net effect of these two terms in the square bracket is the *per-capita* growth rate $r_i = \frac{1}{p_i}\frac{dp_i}{dt}$ of species *i*. We note that the *per-capita* growth rate is linear with respect to the populations p_j, and, in particular, has the Lotka-Volterra form $r_i = b_i + Q\sum_{j=1}^{n}A_{ij}p_j$. Thus, it has at most one fixed point where all species populations p_i^* are positive, i.e., a coexistence steady state. This steady state is given by

$$p_i^* = -\sum_{j=1}^{n}(\boldsymbol{A}^{-1})_{ij}\left(b_j/Q\right) = -\sum_{j=1}^{n}(\boldsymbol{A}^{-1})_{ij}\left(c_jS - m_j/Q\right), \quad (4)$$

where $(\boldsymbol{A}^{-1})_{ij}$ is the (i,j)th entry of the inverse of the effective interaction matrix

A. In Appendix S2: Section S1 and Section S2, we prove that as long as the matrix ***H*** is fully hierarchical ($H_{ij} = 1$ if $i < j$ and 0 otherwise), any feasible equilibrium point is stable (similar to Liao et al. 2022). Thus, it is straightforward to compute steady-state communities for a given parameter set and levels of habitat loss and fragmentation (see code in Liao, 2023). To establish a C-C tradeoff, species are first ordered by competitive ability, i.e., with species 1 the best competitor and species n the worst. Then species colonization rates are set in the reverse order, i.e., $c_1 < c_2 < c_3 < \cdots < c_n$ (Tilman, 1994).

The diversity of the steady-state communities is measured using two indices: species richness 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). The inverse Simpson index accounts for variation in species richness and evenness (i.e., the similarity in species' relative abundances), and thus is superior to raw species richness as a measure for diversity (Stirling & Wilsey, 2001; dos Santos et al., 2011). Note that species with steady-state abundance less than 10^{-6} are treated as extinct, since such populations are typically eliminated by environmental fluctuations.

Results

We first consider initial communities of varying species richness (n=3, 4, 5 and 6) with a strict C-C tradeoff. Species colonization rates c_i are taken from arithmetic or geometric sequences, to ensure that all species considered are present in the undamaged landscape ($S = Q = 1$; i.e., starting with an intact community). For an arithmetic sequence (Figure 1A-H), neither species richness nor the inverse Simpson index increases in a simple monotonic fashion with decreasing habitat destruction. Instead, we observe multiple bands where diversity is high, separated by bands where it is low. These bands form across the two components of habitat destruction, habitat loss and fragmentation, thus we can simplify our analysis by considering how biodiversity varies along a single gradient on which habitat destruction decreases, e.g., $S = Q$ (Figure 1: dashed lines). In this form, the bands described above become a sequence of multiple peaks and troughs (Figure 2A-H: blue lines). The number of these peaks increases as initial community size increases (cf. the number of the bands in Figure 1). We obtain similar oscillations in the inverse Simpson index when species colonization rates follow a geometric sequence (Figure 1I-P and Figure 2A-H: yellow lines). Yet, species richness declines monotonically in this case, as raw species richness is insensitive to changes in species abundances.

The multi-peaked biodiversity response emerges from patterns in how the relative abundances of the species in the community change with habitat destruction ($S = Q$ in Figure 2 I-P). We observe that species diversity rises and falls several times along the gradient of habitat destruction. The points on the habitat destruction gradient at which a species enters or leaves the system are "turning points". At these points, trends in abundance reverse, with species in decline starting to increase in abundance and *vice versa*, forming a zig-zag pattern. As such, whenever some species are high in relative abundance but others are low, species diversity is low due to extreme unevenness. Note that, the inverse Simpson index does this by design, while the treatment of populations below a certain abundance threshold as extinct artificially reduces the species richness. Conversely, whenever species' relative abundances are similar, species diversity is boosted by high evenness. Therefore, it is natural that this zig-zag pattern would translate to an oscillating diversity profile (compare Figure 2 A-H with I-P).

The oscillations in species relative abundances ultimately arise from the interaction between habitat destruction and C-C tradeoffs (Figure 2 I-P). Habitat destruction (increasing habitat loss and/or fragmentation) decreases the abundance of the best competitor (species 1) as it has the lowest colonization rate, resulting in species 1 being the first to become extinct. Due to a release in competition pressure, 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 habitat destruction. If the effect is strong enough to reverse trajectories, then oscillating patterns of species relative abundances emerge along the habitat destruction gradient (see mathematical proof in Appendix S3: Section S1; cf. Liao et al., 2022).

Up to now, we have only considered a small number of species (n=3, 4, 5 & 6) in the C-C tradeoff system. However, we continue to observe multiple biodiversity peaks along the habitat destruction gradient in a significantly larger community with n=25 (Figure 3). Furthermore, when either habitat connectivity (Figure 4 A-B & E-F) or habitat availability (Figure 4 C-D & G-H) is fixed, we observe that both diversity indices oscillate strongly as the other component of habitat destruction varies. Again, for its insensitivity to changes in species abundances, species richness does not capture these oscillatory behaviours when species colonization rates are geometrically spaced (Figure 3B and Figure 4B & D). Finally, we observe that community biodiversity ultimately declines for high levels of habitat destruction regardless of model parameters or biodiversity index used.

Our predicted oscillatory responses of biodiversity to habitat destruction are also robust (albeit somewhat weaker) when the strict competitive hierarchy is weakened (Appendix S4: Figure S1) or even violated (Appendix S4: Figure S2). Besides relaxing the fully competitive hierarchy, we further look at a completely different competitive structure: *intransitive competition* (see details in Rojas-Echenique & Allesina, 2011). Using simulations, we find that relatively strong intransitive competition structures produce similar, though less pronounced, oscillating patterns in biodiversity (Appendix S4: Figure S3). This is because we do not impose a global C-C trade-off in these simulations, but rather local C-C trade-offs involving only a subset of the species in the system created at random.

Discussion

Our model demonstrates that multiple peaks in biodiversity emerge naturally along the habitat destruction gradient. This outcome suggests that the prevailing intuition of habitat destruction causing a monotonic decline in biodiversity (reviewed by Fahrig, 2003, 2017) fails to capture the full complexity of the relationship between habitat destruction and biodiversity. This complex response is relatively generic, requiring only the common assumption of a tradeoff between competitive ability and colonization rate. The C-C tradeoff permits species coexistence because superior competitors, which would otherwise dominate the system, are less able to spread in fragmented habitats, due to their low colonization rates (Tilman, 1994; Tilman et al., 1994, 1997). This leaves more space available for those inferior competitors with higher colonization rates, thereby promoting coexistence. However, how many species can coexist stably is determined by the number of species that have appropriate C-C tradeoffs, which are greatly mediated by habitat destruction. Thus, the interaction between habitat destruction and C-C tradeoffs, which facilitates different subsets of species to coexist, creates the multi-peaked biodiversity pattern.

The oscillatory response of biodiversity to habitat loss supports early theoretical results that the number of species that can coexist along a habitat loss gradient does not necessarily change in any simple monotonic fashion (Hastings, 1980; Nee & May, 1992; Tilman et al., 1997). Despite the complex response, the overall trend of habitat loss decreasing species richness still holds, in line with empirical observations (Chase et al., 2020). Interestingly, such oscillating patterns in biodiversity can explain the mixed responses of species richness to habitat fragmentation *per se* observed in nature (Fahrig, 2017; Riva & Fahrig, 2023), thereby providing a new paradigm that can reconcile the debate on the FDR (Fletcher et al., 2018; Fahrig et al., 2019). Note that, it is still difficult to use existing empirical data (see meta-analysis by Chase et al., 2020; Riva & Fahrig, 2023) to definitively confirm these predicted oscillating patterns, as detecting these patterns would require biodiversity measures along high resolution habitat loss and fragmentation gradients.

The oscillatory response of biodiversity to habitat destruction apparently arises from the oscillations in species relative abundances, but ultimately comes down to the asymmetric control mechanism in the C-C tradeoff community. Specifically, if a strong competitor is present at high abundance in the hierarchical competitive community, it will suppress the abundance of all weaker competitors. However, the species directly below it in the competitive ranking will be suppressed most as it gains the least compensation for its competitive inferiority from its advantage in colonization rate. This, in turn, benefits the species one step further down the competitive ranking. This is why the abundance peaks of adjacent species tend to alternate. Reducing the level of habitat destruction favours stronger competitors, as it reduces the disadvantage of lower colonization rates. Consequently, as the habitat conditions improve, competitors are introduced to the community in sequence (from weakest to strongest). When a new competitor is introduced, it suppresses the next strongest competitor with effects that propagate through the rest of the community. As such, these processes would repeat more times in species-richer communities, thereby resulting in multiple peaks in species diversity along the habitat destruction gradient.

So far, the complex response of biodiversity to habitat destruction has been ignored in most empirical observations, for several reasons. Firstly, empirical work often tried to take a small range or several levels of habitat destruction as representative of the effect of its full range, thus individual studies are unlikely to be able to observe the complete pattern which gives rise to specific responses. Secondly, it is also unusual to observe a community over sufficiently long periods for a stable community to emerge (Shea et al., 2004). This could result in a short-term decline in diversity, due to the disruption of habitat destruction, being taken as the long-term effect, thereby ignoring the possibility of emergence of other species in the community. Finally, the prevailing *a priori* intuition that the effects of habitat destruction are always negative, could lead ecologists to disregard positive responses, by considering them as the noise arising from experimental error or system stochasticity. Despite these empirical limitations, the increased sample size offered by Riva & Fahrig (2023) allows to be reasonably confident that positive biodiversity responses to habitat fragmentation *per se* are also very common and even outweigh negative responses, thus we should not disregard these unexpected positive cases. Furthermore, our model offers a parsimonious mechanistic explanation for these empirical observations on the FDR, which should provide ecologists with confidence to accept a broader range of possible responses.

It should be noteworthy that this mean-field approximation model only elucidates the C-C tradeoff mechanism, which is relatively simple. In fact, there are many mechanisms at play affecting biodiversity when habitat is fragmented instead of being continuous (Fahrig et al., 2022; Fletcher et al., 2023; Riva & Fahrig, 2023). For instance, so-called geometric effects, emerging from species clustering and distance-decay in community similarity, have been often proposed as a key mechanism underlying positive FDRs (May et al., 2019; Riva & Fahrig, 2022). For model simplicity and mathematical tractability, we further assume that there is no any dispersal among habitat fragments. This assumption is relatively restrictive, as in many natural metacommunities where species vary substantially in dispersal ability, some superior dispersers can cross the habitat matrix between adjacent fragments to recolonize lost habitats. Thus, future study could include more realistic species dispersal among fragments, which would affect the species diversity we predict at the landscape scale. However, when species dispersal between fragments is highly limited (e.g., blocked by physical barriers) so that it is insufficient to affect local community dynamics, our predicted oscillatory responses of biodiversity to habitat destruction have important implications for biodiversity conservation. For example, increasing habitat connectivity (e.g., constructing ecological corridors) as the typical conservation activity might risk further species losses, if carried out without first analyzing their potential consequences. In addition, biodiversity, the goal of conservation, is not necessarily itself a good measure of conservation success. To give an analogy: a growth burst in a fish stock which is otherwise near collapse, does not mean that the fish population is stable. Rather, the increased population size is likely a temporary phenomenon arising from the increase in fluctuation variance near a tipping point (Scheffer et al., 2001; Drake & Griffen, 2010). Thus, while what we care about is the stock size, this size itself may be a poor indicator of the fishery's future success. Similarly, given a highly oscillatory FDR, an observed burst in biodiversity does not mean that the system would be able to tolerate even more habitat fragmentation. Consequently, the success of conservation actions should be evaluated not only on changes in biodiversity, but also on the sensitivity of the system to changes in habitat connectivity. Furthermore, the strongly oscillatory response of biodiversity to fragmentation *per se* provides new insights into the long-standing debate on whether protecting biodiversity is better achieved using a Single Large Or Several Small (SLOSS) reserves (Diamond, 1975; Simberloff & Abele, 1976; Fletcher et al., 2018; Fahrig et al., 2019), as we find that it is a complex function of the competitive structures, species demographic traits and landscape fragmentation properties. Therefore, identifying these ecological factors from empirical data is an essential precursor to setting conservation priorities in applied ecology.

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Figures and captions

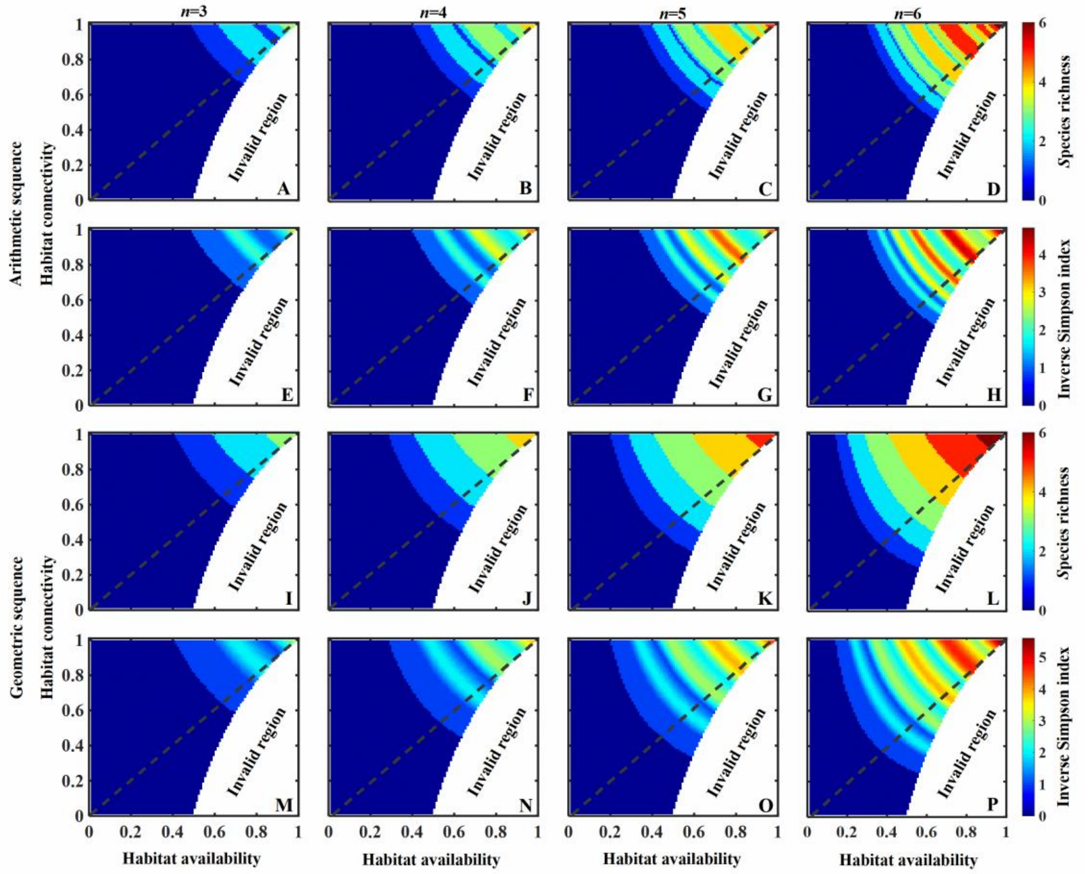

Figure 1. Interactive effects of habitat availability (S) **and connectivity** (Q) **on species diversity**, in multispecies communities (n=3, 4, 5, 6) with a strict competitive hierarchy $\boldsymbol{H}$ (H_{ij}=1 for i<j and 0 otherwise). In particular, all species considered are present in the undamaged landscape (i.e., starting with an intact community at $S = Q = 1$). Species diversity is characterized using richness (A-D & I-L) and the inverse Simpson index (E-H & M-P). Dashed lines indicate the randomly structured landscapes with $S = Q$. Species colonization rates are set to obey: (A-H) the arithmetic sequence $c_i = c_1 + 0.045 \times (i-1)$ and (I-P) the geometric sequence $c_i = m/(1-q)^{2i-1}$ with $q = 1 - m/c_1$. Other parameters: c_1=0.12, and mortality rates $m = 0.1$ for all species. Invalid region: $2 - 1/S < Q < 1$.

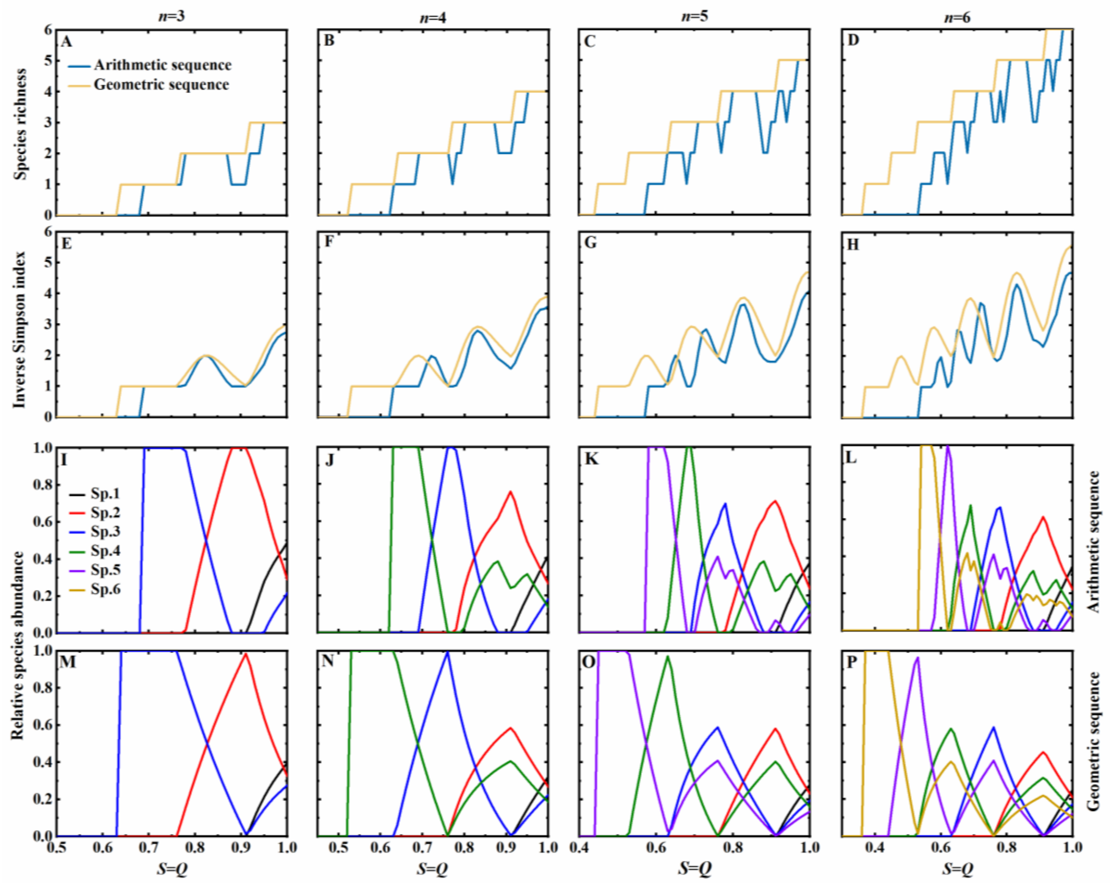

Figure 2. Effects of varying habitat availability and connectivity simultaneously (i.e., randomly structured landscapes with S=Q, as indicated by dashed lines in Figure 2) on species diversity (A-H) and relative species abundances (I-P) in multispecies systems (n=3, 4, 5, 6) with a strict competitive hierarchy (H_{ij}=1 for i<j and 0 otherwise). Species diversity is characterized by species richness (A-D) and the inverse Simpson index (E-H). All parameter settings are seen in Figure 1.

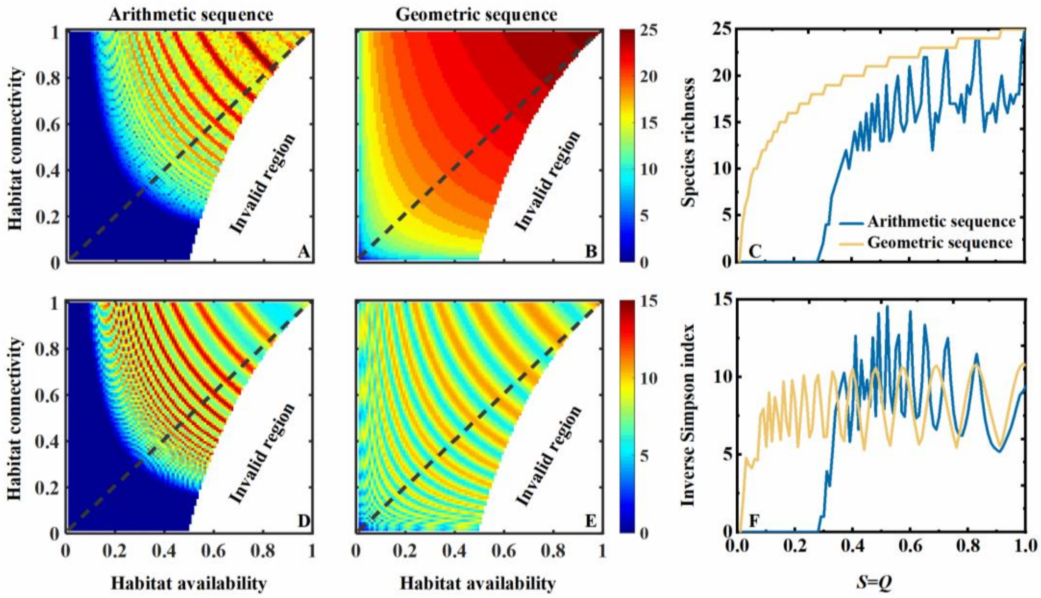

Figure 3. Interactive effects of habitat availability(*S*) and connectivity (*Q*) on species diversity in a large community of *n*=25 with a strict competitive hierarchy. Again species diversity is characterized by species richness (A-C) and the inverse Simpson index (D-F). In particular, all species considered are present in the undamaged landscape (i.e., starting with an intact community at S=Q=1), by setting species colonization rates to follow (A & D) the arithmetic and (B & E) geometric sequences respectively. Panels (C & F) correspond to the cases with *S*=*Q* (i.e., randomly structured landscapes) in panels (A & B) and (D & E), respectively, as indicated by dashed lines. All parameter settings: see Figure 1.

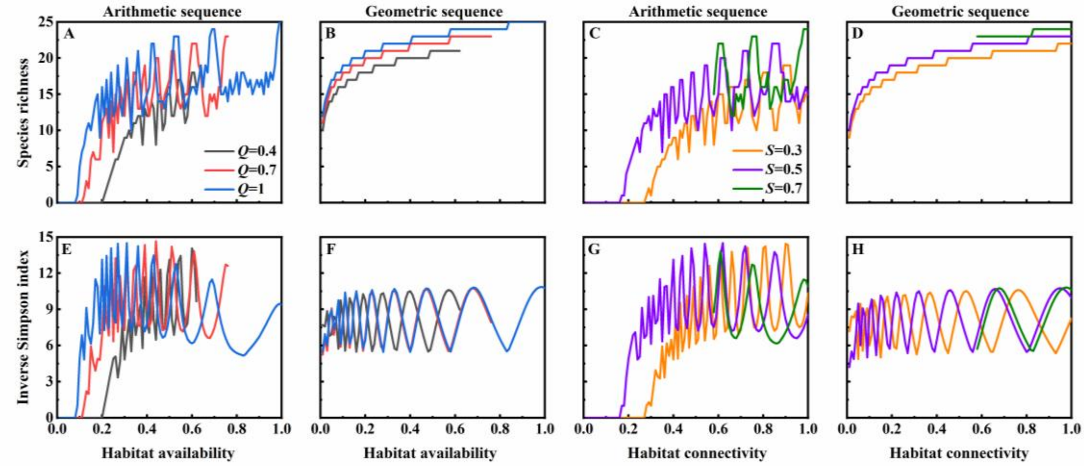

Figure 4. Individual effects of habitat availability(*S*) and connectivity (*Q*) on species diversity **in a large community of *n*=25.** Species diversity is characterized by species richness (A-D) and the inverse Simpson index (E-H). Other parameter settings are seen in Figure 3.