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Habitat loss alters effects of intransitive higher-order competition on biodiversity: a new metapopulation framework

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Abstract

Recent studies have suggested that intransitive competition, as opposed to hierarchical competition, allow more species to coexist. Furthermore, it is recognized that the prevalent paradigm, which assumes that species interactions are exclusively pairwise, may be insufficient. More importantly, whether and how habitat loss, a key driver of biodiversity loss, can alter these complex competition structures and therefore species coexistence remain unclear. We thus present a new simple yet comprehensive metapopulation framework which can account for any competition pattern and more complex higher-order interactions (HOIs) among species. We find that competitive intransitivity increases community diversity and that HOIs generally enhance this effect. Essentially, intransitivity promotes species richness by preventing the dominance of a few species unlike hierarchical competition, while HOIs facilitate species coexistence through stabilizing community fluctuations. However, variation in species vital rates and habitat loss can weaken or even reverse such higher-order effects, as their interaction can lead to a more rapid decline in competitive intransitivity under HOIs. Thus, it is essential to correctly identify the most appropriate interaction model for a given system before models are used to inform conservation efforts. Overall, our simple model framework provides a more parsimonious explanation for biodiversity maintenance than existing theory.

Keywords: habitat loss, higher-order interactions, intransitive competition, metapopulation model, pairwise competition, site-occupancy dynamics.

1. Introduction

Despite interspecific differences in competitive ability, the high levels of biodiversity present in ecological communities is a long standing mystery in community ecology [1-4]. Classical modelling approaches demonstrate that competition between species pairs often drives one species to extinction (competitive exclusion). Furthermore, theoretical studies for large communities predict that community stability declines as the number of species increases [5]. Consequently, established explanations for community diversity rely in large part on exogenous factors which shape the community. Such factors include niche-structured habitats, which permit species to coexist through inhabiting different niches (niche theory [3]), or the existence of a global metacommunity, in which all species coexist and from which local communities are assembled by dispersal processes (neutral theory [6]). However, empirical evidence that classical resource-based niche differences are essential for coexistence is rare [7-9], and the species equivalence assumptions of neutral theory are hard to reconcile with nature [10, 11].

An alternative coexistence mechanism is *competitive intransitivity* within the community [12, 13]. This means that the competitive abilities of the species cannot be ordered into a strict hierarchy (hierarchical competition [14]) instead forming competitive cycles (e.g. the rock-paper-scissors game [15, 16]). Recent studies have returned to this concept, noting that it could explain biodiversity maintenance as no single species can outcompete all others [17-22]. More and more empirical evidence of intransitive competition has been found in bacterial, phytoplankton, plant, vertebrate and invertebrate communities [16, 21, 23-27]. For example, Kerr *et al.* [16] showed that intransitive interactions occur between engineered strains of the bacterium *Escherichia coli*, whereas Cameron *et al.* [24] found the parasite-grass-forb intransitive competition, with the dynamics of the system conforming to a rock-paper-scissors game. Additionally, Soliveres *et al.* [21] specifically documented a positive relationship between the degree of intransitivity and species richness. Thus, competitive intransitivity is suggested to play an important role in maintaining species diversity in communities of varying types.

Additionally, the focus in most theoretical studies has been to use the species pair as the fundamental unit of study (pairwise competition). However, in practice complex community patterns and dynamics often cannot be explained solely by pairwise interactions even with competitive intransitivity [28, 29]. This lack of explanatory power has recently been attributed, at least partially, to higher-order interactions (HOIs), i.e. interactions between more than two species simultaneously [29-32]. Theoretical studies suggest that HOIs stabilize the dynamics of species-rich communities [33, 34] and, as such, may promote community diversity in their own right [33-36]. Such interactions have often been ignored previously because there was little empirical evidence for their existence. However, more recent field studies, with superior statistical techniques [37], have shown that HOIs are actually abundant in nature [35]. For instance, a shrub can provide indirect benefits to a grass through suppressing a forb in a shrub-forb-grass interaction chain [35], while Mayfield & Stouffer [37] used direct statistical tests to find that HOIs significantly affect the fecundity of three of six focal plant species by weakening the suppressive effect of neighbours (e.g. from resource/space competition). Although both factors, including intransitive competition and HOIs, play a vital role in maintaining biodiversity, habitat loss, a key driver of biodiversity loss, greatly threatens ecological communities. More importantly, little is known about whether and how habitat loss can alter the effects of intransitive higher-order competition on species coexistence.

Building on classical site-occupancy models [14], we construct a new comprehensive modelling framework for competitive communities encompassing these factors. Specifically, the outcomes of competitive interactions between any pair of species are encoded in a *tournament matrix* [17-20], allowing any possible competitive structure to be represented. Higher-order interactions are incorporated by permitting a fixed number of pairwise interactions to occur within each time unit, providing a relatively simple representation of such interactions [34]. Finally, the underlying site-occupancy model provides a straightforward way to introduce habitat loss, one of the primary drivers of biodiversity loss worldwide. Using this extended model, we explore how these factors: competitive intransitivity, HOIs, and habitat loss, interact to influence community diversity. We show that, while competitive intransitivity always has a positive effect on community diversity, the effect of HOIs depends on other factors.

2. Methods

2.1. Metapopulation model for pairwise competition

On the landscape scale, the dynamics of populations are typically modelled using the site occupancy, or metapopulation, framework [14, 38-40]. It is assumed that the landscape is divided into a finite number of colony sites and that population sizes can be measured in terms of the number of sites that a species occupies. Implicitly, this means that each colony site can only accommodate one single individual of a species. Population growth occurs when new colony sites are established (*colonization*) and the population decreases when an individual dies out (*mortality*). Each individual produces colonizers (e.g. seeds or excess individuals) which can establish new colonies. Thus, a species can be regarded as exerting a *colonization pressure* proportional to its population size on the other colony sites within the landscape.

There are a variety of ways to model competition between species. In this study, we assume that, on the time scale of the model, coexistence between species within a colony site is impossible. Thus, competition is represented by allowing colonizers of one species to displace an individual of another species (*competitive invasion*). The probability (or rate) of competitive invasion is determined by comparing the relative competitive strength of the species involved.

With these assumptions in mind, a community of n species can be modeled using a system of equations of the following form (electronic supplementary material, *Model derivation* in *Appendix A*)

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

Here p_i, c_i, and e_i represent: the fraction of sites occupied by species i; the rate at which an individual of this species produces colonizers (colonization rates); and the rate at which individuals of this species die out (mortality rates), respectively. The terms in Eq. (1) describe how the population changes due to the three processes: colonization, mortality, and competitive invasion described above. Species mortality occurs at a constant rate e_i, thus the expected change in site occupancy is given by multiplying this rate by the fraction of occupied sites p_i. Similarly, colonizers are produced at a constant rate c_i, so the colonization pressure is given by $c_i p_i$. However, not all sites are available for colonization, thus we multiply by the rate at which a colonizer moving at random would find an unoccupied site. This is expressed in terms of the fraction of sites occupied by any species $\left(\sum_{j=1}^{n} p_j\right)$ and, possibly, the fraction of habitat sites that are unsuitable for any species establishment (U - habitat loss).

Finally, competitive invasions occur when a colonizer from one species finds a site occupied by a species and displaces it. The terms H_{ij} and H_{ji} are the probabilities that species i displaces species j and that species j displaces species i respectively, and are typically regarded as mutually exclusive, e.g. $H_{ij} + H_{ji} = 1$ and H_{ii}=0.5 if i=j [19, 34]. The probabilities for the whole system can be encoded in a *tournament matrix H*. Thus, the invasion term is given by a sum of the net result of pairwise competition events, where species i displaces or is displaced by another species j, which in turn depend on the competition pressure exerted by, and the population size of, these species.

If the vital rates of all species are assumed to be the same ($c_i = c$ and $e_i = e$), Eq. (1) simplifies to

$$\frac{dp_i}{dt} = cp_i\left(1 - U - \sum_{j=1}^{n} p_j\right) - ep_i + cp_i\sum_{j=1}^{n}(H_{ij} - H_{ji})p_j. \qquad (2)$$

After some straightforward algebra (see electronic supplementary material, *Appendix A*), Eq. (2) can be rearranged to obtain

$$\frac{dp_i}{dt} = cp_i\left(1 - U - p_i + \sum_{j \neq i}^{n} M_{ij}p_j\right) - ep_i, \qquad (3)$$

with the matrix *M* having elements $M_{ij} = H_{ij} - H_{ji} - 1$. Thus, the site occupancy of species *i* at equilibrium is given by $p_i^* = \left(1 - U - \frac{e}{c}\right) + \sum_{j \neq i}^{n} M_{ij}p_j^*$ if $\sum_{j \neq i}^{n} M_{ij}p_j^* > \frac{e}{c} - (1 - U)$. Otherwise, $p_i^* = 0$ and the model predicts the extinction of species *i*. Classical analytical results for two- or three-species systems [13, 14, 38] can be reproduced in this system (electronic supplementary material, *Appendix A*).

2.2. Extension for higher-order competition

Given that colonization pressure is applied globally within a landscape, it is reasonable to assume that competitive invasions are not necessarily strict pairwise events. For example, it is possible that different species might simultaneously invade a site occupied by another species. The simplest resolution of such a case is to determine the final state of the site from sequential pairwise competition between the species involved [34]. Note, in particular, that this approach does not model the typical HOI paradigm [33] where interspecific interactions vary depending on which species are present. In our setting, the higher-order aspect arises simply from the necessity of tracking a sequence of competitive events, i.e. where two species compete and the winner then competes with a third, which does not affect the final competitive outcome. Thus, these HOIs summarize the outcomes of processes that occur on faster time scales than the overall timescale of the metapopulation framework, emphasizing effects of discordances in the temporal scales of competitive processes.

It is relatively straightforward to incorporate three-way sequential pairwise competition [34] into the existing framework obtaining

$$\frac{dp_i}{dt} = c_i p_i\left(1 - U - \sum_{j=1}^{n} p_j\right) - e_i p_i + \sum_{j,k=1}^{n}\left(2c_i H_{ij} H_{ik} - c_j H_{ji} H_{jk} - c_k H_{ki} H_{kj}\right) p_i p_j p_k$$

.(4)

The only difference between this equation and Eq. (1) is in the competitive invasion term where we now consider the outcomes of invasions of sites occupied by species *i*, *j*, and *k* in a similar way to that explained above. The asymmetry in the numerical coefficients of the invasion term (2,1,1) arises from the fact that species *i* could compete with species *j* to invade a site occupied by species *k* or vice versa with species *k* to invade a site occupied by species *j*. As such, there are more sequential contests in species-richer communities because of more combinations of the triple-wise interaction.

As previously, if the vital rates of all species are assumed to be equal, Eq. (4) simplifies to give

$$\frac{dp_i}{dt} = cp_i\left(1 - U - \sum_{j=1}^{n} p_j\right) - ep_i + cp_i \sum_{j,k=1}^{n}\left(2H_{ij} H_{ik} - H_{ji} H_{jk} - H_{ki} H_{kj}\right) p_j p_k, (5)$$

and, furthermore, can simplified to obtain

$$\frac{dp_i}{dt} = cp_i\left(1 - U + \sum_{j,k}^{n} T_{ijk} p_j p_k - p_i - \sum_{j \neq i}^{n} p_j\right) - ep_i, \tag{6}$$

where the matrix T has elements $T_{ijk} = 2H_{ij}H_{ik} - H_{ji}H_{jk} - H_{ki}H_{kj}$ (see electronic supplementary material, *Appendix A*). Thus the site occupancy for species i at equilibrium is given by $p_i^* = \left(1 - U - \frac{e}{c}\right) + \sum_{j,k}^{n} T_{ijk} p_j^* p_k^* - \sum_{j \neq i}^{n} p_j^*$, if $\sum_{j,k}^{n} T_{ijk} p_j^* p_k^* - \sum_{j \neq i}^{n} p_j > \frac{e}{c} - (1 - U)$ and is 0 otherwise.

2.3. Measurement of competition within a community

In two-species communities, either one species is a stronger competitor than the other, i.e. $H_{ij} > H_{ji}$ denoted *i* > *j*, or the species have equal competitive ability ($H_{ij} = H_{ji} = 0.5$). This is a simple hierarchical pattern. However, when a third species is added, a fundamentally new possibility is created. In particular, it is possible for the competition to be hierarchical, e.g. *i* > *j* > *k*, or competition can be cyclic, e.g. *i* outcompetes *j* which outcompetes *k* which outcompetes *i*, denoted *i* > *j* > *k* > *i* (similar to the rock-paper-scissors game). These patterns are described as *transitive* or *intransitive* competition respectively.

Thus, competition within an *n*-species community has at least two measurable aspects. Firstly, there is the degree to which the elements of the tournament matrix *H*, i.e. the competition strengths H_{ij}, vary within the community. At one extreme, all species are competitively equal (neutral competition with $H_{ij} = 0.5$); at the other, any pairwise competition event has a certain winner and loser (i.e. $H_{ij} = 0$ or 1). This is summarized by the coefficient of variation $C.V.(H) = \frac{\sigma_H}{\overline{H}}$ with σ_H being the standard deviation for all elements H_{ij} and $\overline{H}$ the mean of these elements.

Secondly, the degree of intransitivity can be quantified using the relative intransitivity (*RI*) index of the tournament matrix *H*. This is given by [20]

$$RI = 1 - \frac{Var_{obs} - Var_{min}}{Var_{max} - Var_{min}}. \qquad (7)$$

Here, Var_{obs} denotes the variance of the row sums, $h_i = \sum_{j=1}^{n} H_{ij}$ or score sequence, of the tournament matrix *H*. Var_{max} and Var_{min} are the maximum and minimum possible variances for the row sums of a competitive tournament matrix with the same number of species as the observed tournament matrix respectively. The minimum variance Var_{min} for the score sequence is obtained when the row sums are as uniform as possible. High row sum variance means that a few species win the majority of competitions, and hence corresponds to transitive competition. Low row sum variance means all species have similar numbers of species that they can outcompete, i.e. intransitive competition. When Var_{obs} is close to Var_{max}, a low *RI* index is obtained, indicating that transitive competition is prevalent in the community. When Var_{obs} is close to Var_{min}, a high *RI* index is obtained. Note that when $C.V.(H)$ is low, all rows are similar and thus a high *RI* index is always obtained.

2.4. Numerical simulations

Numerical methods (ODE45, Matlab 2016a) were used to determine the non-trivial steady states (and hence the system diversities) for multi-species competitive systems (see electronic supplementary material, figures S1-S4 in *Appendix B* and Matlab codes in *Appendix C*). Simulations were run until initial transients had dissipated and the long term system state had been reached (e.g. either reaching a fixed point or a periodic cycle). Species were assumed to be functionally extinct if the minimum site occupancy at steady state (normally from 10,000~20,000 time steps) fell below 10^{-4}. Each system was run for 20 replicates to establish the generic behaviour of the system as opposed to that which could emerge from a specific set of initial conditions.

To further test the robustness of these steady states, a continuous stochastic environmental perturbation $W_i(t) = \Omega \times [1 - 2 \cdot \delta(t)] \cdot p_i(t)$, with Ω being the perturbation size/amplitude ($\Omega = 0.1$), $\delta(t)$ a uniform random variate that varies temporally between 0 and 1 (i.e. $\delta(t) \sim unif[0, 1]$), and $p_i(t)$ the site occupancy of species *i* at time *t*, was incorporated directly as a stochastic component of the deterministic systems described above (i.e. stochastic differential equations, SDEs), similar to Grilli *et al.* [34]. As shown in figures S5-S7 (electronic supplementary material, *Appendix B*), both stochastic and deterministic models yield qualitatively similar trajectories in most cases; with stochastic fluctuations around the deterministic dynamics. Only for neutral models (equal vital rates and either no competition or equal competition ability for all species) do stochastic perturbations produce non-trivial effects. In particular, while the deterministic model predicts high species diversity in such cases, stochastic perturbations eventually lead to dominance by a single species.

The effect of the following factors: variation in competition strength $C.V.(H)$; intransitivity of competition (*RI*); the degree of habitat loss (*U*); and the number of species in the initial community (*n*), on community diversity was then explored. Specifically, distinct systems were generated by systematically varying these parameters. The resulting community diversity was then found and related to the controlled parameter. This is straightforward for U and n, but $C.V.(H)$ and RI require more explanation (see below). Additionally, cases where all species within the community had the same vital rates and cases where these vital rates were permitted to differ between species were considered separately.

The effect of variation in competition strength $C.V.(H)$ was explored (see figure 1) by randomly generating tournament matrices H subject to the condition that $H_{ij}+H_{ji}=1$. Each matrix H was randomly constructed using the given two elements {0.5, 0.5}, {0.49, 0.51}, {0.48, 0.52}… {0, 1} respectively with 0.01 increments around the mean competition strength $\overline{H}=0.5$. The coefficient of variation $C.V.(H)$ was computed for each realized system. Note that, in such randomly-structured matrices, competitive intransitivity is generally very high ($0.9 < RI < 0.98$) (see electronic supplementary material, figure S8 in *Appendix B*). To verify the generality of the outcome, we additionally constructed another type of random tournament matrices H (electronic supplementary material, figure S9 in *Appendix B*), where one element in each pair of competitors *i-j* was produced randomly from a uniform distribution with range varying from [0.49, 0.51] to [0, 1] (with 0.01 increments) and the second determined from it ($H_{ij}+ H_{ji}=1$).

As such, to assess the effect of RI, it is necessary to choose a tournament matrix H with high variation in competition strength ($H_{ij}= 0$ or 1) and permute it [20]. First a matrix with purely hierarchical competition was constructed ($1>2>3>\cdots>n$), containing all ones above the diagonal and all zeros below the diagonal. Then, the interaction between each pair of species (*i, j*) was reversed with probability *f*, a random perturbation of the tournament matrix. This probability *f* was taken from the following set of values {0, 0.05, 0.1, 0.15…0.95, 1}, yielding a broad range of *RI* values.

In systems where vital rates were permitted to vary within the community, the c_i's and e_i's were drawn randomly from uniform distributions with ranges *unif*[0.6,1] and *unif*[0,0.2] respectively. To test the robustness of these outcomes, a broad range of biologically reasonable parameter combinations were explored (electronic supplementary material, figures S8-S14 in *Appendix B*) and found to yield qualitatively similar outcomes (e.g. effects of variation in species vital rates in electronic supplementary material, figure S11 in *Appendix B*), thus allowing us to present our general results in figures 1-4 by choosing a single reference case. In this study, we attempt to check whether there is any difference in the competitive outcome between pairwise and higher-order competition in landscapes with habitat loss by varying species vital rates.

3. Results

3.1. Intransitive competition promotes diversity when differences in competitive ability are large

In the long term, a community where all species have identical vital rates and equal competition strength (a neutral community), will be dominated by a single species (figure 1 V-VIII; electronic supplementary material, figure S5 in *Appendix B* and system analysis in *Appendix A*). However, introducing a small random variation in competition strength allows a coexisting sub-community to emerge. Community diversity declines, to a greater or lesser extent depending on other factors, but eventually saturates at higher levels than can be obtained in the neutral community. If the colonization and mortality rates of species within the community differ, the effect of a small variation in competition strength is less dramatic (figure 1I-IV). Instead, community diversity increases gradually as variation in competition strength increases, saturating at levels slightly lower than those seen in communities with no variation in vital rates.

As noted previously, in order to investigate the full range of possible relative intransitivity (*RI*) values, it is necessary to fix variation in competition strength at a high level. If the outcome of any competitive interaction is certain ($H_{ij} = 0$ or 1), increasing the *RI* degree also increases community diversity (figure 2). The relationship contains two ranges where diversity increases quickly, for low levels of relative intransitivity and then for high levels of relative intransitivity, separated by an intermediate range where diversity increases slowly, although note that these ranges become more or less distinct depending on other factors. This relationship can be well described by a degree 3 polynomial. Thus, this suggests that intransitivity in competition between species enables greater diversity within the community. Note that random community structures display very high *RI* levels (electronic supplementary material, figure S8 in *Appendix B*) and, as such, ecological communities are likely to have this property.

However, competitive intransitivity is not sufficient to ensure high community diversity. When all species are equal competitors, i.e. variation in competition strength is 0 (figure 1), competition is intransitive yet community diversity is low. Furthermore, when variation in competition strength is low, the effect of intransitive competition can be overwhelmed by variation in the other vital rates of species (cf. figure 1 I & V). In this case, as variation in competition strength increases, community diversity increases. These trends suggest that the effect of intransitive competition on diversity depends on the degree to which competition strength varies within the community.

3.2. Predictions of community diversity are dependent on the complexity of competition

There are pronounced differences in the effects of competition on community diversity dependent on whether competition occurs pairwise or as a three-way interaction (figures 1 & 2). Specifically, for models with no variation in vital rates, there is a pronounced increase in community diversity when HOIs are included. However, this difference is significantly reduced when other vital rates are chosen randomly for each species (figures 1 & 2; electronic supplementary material, figures S9 & S11 in *Appendix B*); although the overall trends are preserved.

As can be expected, increasing levels of habitat loss, decreasing habitat availability, reduce community diversity. However, again differences emerge depending on whether pairwise or higher-order competition is considered (figures 2 & 3). When vital rates are permitted to vary, higher-order competition produces higher diversity than pairwise competition for low levels of habitat loss, but this reverses for high levels of habitat loss. This switch in predicted outcome is not observed if all species have the same vital rates, where HOIs always maintain higher species diversity than pairwise competition (electronic supplementary material, figure S14 in *Appendix B*).

3.3. Community diversity declines with initial community size

Finally we test the effect of initial community size on the fraction of species that can coexist in the competitive system (figure 4). Regardless of variation in vital rates, the fraction of survival species declines as the initial number of species increases. This decline is approximately linear with respect to the log-scale of the initial number of species, indicating a simple reciprocal relationship. This outcome can be explained as a combination of two factors. Firstly, a finite number of species can coexist (determined by the other factors discussed), and the observed decline is a natural consequence of computing diversity relative to the initial number of species in the community. Secondly, the more species the initial community has, the less likely it is that a transitive competitor will be present at a higher position in the competitive hierarchy than species that are part of a stable intransitive sub-network (see figure S8 in *Appendix B*). Thus, larger communities favor an intransitive competition structure and hence lower diversity.

4. Discussion

In this study we present a general framework for modelling the landscape scale dynamics of a community with direct competitive interactions. Metapopulation models were initially developed to investigate community assembly arising from the interplay of colonization and mortality processes in finite habitats [41]. Since then the framework has often been used to describe direct competition between species with a specific, typically hierarchical, structure [14]. These studies have shown that a tradeoff between colonization and competition ability can maintain community diversity within the landscape. However, an increasing number of empirical studies have observed intransitive competition structures in natural communities [16, 21, 23-27], suggesting that an alternative paradigm is required. The more general framework used in this study readily allows a broad range of different competition structures to be explored. In doing so we find that intransitive, e.g. cyclic, competition structures, associated with HOIs, facilitate species coexistence (figures 1 & 2). Essentially, intransitivity promotes species richness by reducing interspecific difference in cumulative interactions (including positive and negative) and therefore mitigating competitive exclusion, as those species subject to decreased negative cumulative interactions remain viable in the system. In addition, HOIs facilitate species coexistence through decreasing population fluctuations and thus stabilizing community dynamics compared to pairwise competition (electronic supplementary material, figures S1-S4 in *Appendix B*), similar to Grilli *et al.* [34].

Intransitive, rather than hierarchical, competition structures mean that there is no single dominant species, or group of species, which outcompete the others. Instead, each species outcompetes some species and is outcompeted by others. As such, decreasing the abundance of any competitor in the intransitive loop propagates through the competitive network in a manner that feeds back to favor the recovery of the perturbed species. This creates dynamic species-specific niches within the landscape; sites occupied by species that a given species can outcompete represent opportunities for that species to expand. If all species have similar competition ability, with only small advantages and disadvantages, these niches are only weakly differentiated, while, if differences in competition ability are large, these niches become more pronounced. Thus, the effects of competitive intransitivity can be understood in terms of niche theory, in that clearly defined niches promote community diversity. However, this niche creation is actually a result of the interplay of species interactions and environmental constraints [42]. Competitive intransitivity could, for example, arise in a situation with three limiting resources and three consumers, and each consumer is superior in competing for a different resource [43, 44]. By manipulating the relative resource supply rates, the phenomenological competitive pattern could easily shift from a transitive to an intransitive one, determined by the external environment. As such, it presents a welcome unification of neutral and niche theories, allowing the assembly of diverse communities. Besides the niche difference, the outcome of intransitive competition promoting species coexistence can also be explained by the fitness difference among species in the context of Chesson’s coexistence theory [3, 45, 46]. There exists a large difference in species fitness in strict hierarchical competitive communities, in contrast to the intransitive competition structures in which all species have similar fitness. Thus, differences in the fitness of those species drive competitive exclusion, with large differences suppressing coexistence. Recently, an increasing number of empirical studies have observed competitive intransitivity in natural communities [16, 21, 23-27], supporting the conclusion that intransitive competition may be an alternative mechanism driving community diversity. However, we should note that intransitive rather than hierarchical structure is considerably more probable in random competition matrices (electronic supplementary material, figure S8 in *Appendix B*) and so it is possible these patterns arise by chance.

Perhaps more significantly for ecological applications, community diversity responds differently to habitat loss depending on which type of competition is used in the model. Recent studies have suggested that the existence of HOIs allow more species to coexist than purely pairwise interactions [33, 34, 47]. We demonstrate that, while this holds for low levels of habitat loss, at high levels of habitat loss HOIs reduce community diversity. Essentially, an increase of habitat loss associated with variation in species vital rates can lead to a more rapid decline in competitive intransitivity under HOIs (see figure S12 in *Appendix B*). In other words, habitat loss and demographic variation interact to damage intransitive structures and shape more hierarchical competitive communities, thereby accelerating species exclusion. Consequently, it is important to determine which type of interaction is most appropriate for a particular system, prior to basing conservation activities on the predictions of a mathematical model.

We suggest that the relatively long timescales implicit in site-occupancy modelling mean that higher-order competition is more likely to be appropriate. In particular, it is likely that colonizers from multiple species may interact before a new sub-population establishes itself on a specific site. However, pairwise competition may be appropriate for specific ecological systems. It should be noted that previous studies have suggested that higher-order effects may be comparatively rare [30], since it has been commonly argued that effects of pairwise competition are likely to counteract each other in higher-order combinations such that they essentially cancel out [48]. However, this observation does not relate directly to sequential pairwise competition of the type modelled here [34]. Furthermore, given that variation in vital rates can reduce the difference between pairwise and higher-order competition, it may be difficult to distinguish these cases in empirical studies. Interestingly, Worthen & Moore [49] provided some empirical support for this inference, as they documented a significant higher-order effect among mycophagous drosophilids and suggested that the multigenerational laboratory studies may underestimate or obscure the importance of HOIs for community stability.

For mathematical simplicity, we make several assumptions in our model. First, we assume that all species are able to access any site within the habitat. Although more limited dispersal paradigms could be used, it does not change the major qualitative predictions of the spatial competition model [50]. The second assumption used in our model is the division of habitat into suitable and unsuitable sites. In fact, real habitats rarely consist of neatly divided colony sites of “habitat” and “non-habitat”; instead habitat degradation coincides with reduction in habitat quality, so that most habitats show at least some levels of habitat variegation (varying suitability for species). However, since we are less concerned with exogenous niches than those which emerge as a result of species interactions, this is not a significant limitation for this study. The third assumption is that pairwise competition is strictly hierarchical and that no coexistence is possible within a colony site. In practice, local coexistence is possible in many communities, which allows more complex forms of interaction between species [46, 51-53]. Such complexities are beyond the scope of this study, but they might form the basis of future work. Finally, a set of differential equations are used to draw conclusions about an intrinsically stochastic process. However, we find that stochastic perturbations of these systems do not significantly affect the results we present here. Furthermore, several stochastic individual-based simulations on intransitive competition yield qualitatively similar outcomes [20]. Thus, while the model presented here is a simplification of the complexity in nature, it can capture many essential features of competition among species in a physically homogeneous habitat.

The relative simplicity of this model presents the opportunity to use realized species abundance profiles to estimate vital rates and competition structure within communities. However, at present suitable empirical data for such tests does not exist. As such, detailed experimental work designed with these interactions in mind would be beneficial. We suggest that extensions to microcosm experiments [16, 54] or controlled field observations [21, 22, 37], could fill this gap. However, we note that higher-order competition may be difficult to distinguish from pairwise competition outside of highly controlled experiments, due to the confounding effect of variation in other vital rates. Thus, true field studies would need to separate the effects of variation among species from that of the community competition structure. A practical reason why HOIs in general have received less attention than pairwise interactions is due to increasing experimental complexity imposed by collecting data for all subsets of species combinations in a factorial design [48]. However, the type of higher-order competition considered here, which is simply sequential pairwise competition, does not pose this difficulty. Specifically, one could simply assess pairwise interactions between species in a controlled setting and then compare relative abundances in field trials to those predicted by a parameterized model [35].

We introduce a flexible model for incorporating direct competition into the traditional metapopulation model. Our results suggest that this framework unifies aspects of neutral and niche theory, demonstrating that variation in competition between species can create dynamic niches that permit community diversity. Furthermore, to our knowledge, this is the first attempt to compare pairwise and higher-order competition in a metapopulation context. Intransitive competition structures may be an important unrecognized mechanism for community diversity maintenance, and, as such an important factor in future conservation efforts.

Data accessibility: The Matlab codes supporting this article have been uploaded as part of the supplementary material.

Authors' contributions: J.L. designed this study and built the model, Y.L. wrote Matlab codes and analyzed the results, and J.L. & D.B. wrote the manuscript.

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References

[1] Hutchinson GE. 1959 Homage to Santa Rosalia or Why are there so many kinds of animals? *Am. Nat.* **93**, 145-159. (doi:10.1086/282070)

[2] Huston MA. 1994 Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

[3] Chesson P. 2000 Mechanisms of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343-366. (doi: 10.1146/annurev.ecolsys.31.1.343)

[4] Wilson JB. 2011 The twelve theories of coexistence in plant communities: the doubtful, the important, and the unexplored. *J. Veg. Sci.* **22**, 184-195. (doi:10.1111/j.1654-1103.2010.01226.x)

[5] May RM. 1972 Will a large complex system be stable? *Nature* **238**, 413-414. (doi:10.1038/238413a0)

[6] Hubbell SP. 2001 The Unified Neutral Theory of Biodiversity and Biogeography. Monographs in Population Biology. Princeton University Press, Princeton NJ, US.

[7] Adler PB, HilleRisLambers J, Levine JM. 2007 A niche for neutrality. *Ecol. Lett.* **10**, 95-104. (doi:10.1111/j.1461-0248.2006.00996.x)

[8] Levine JM, HilleRisLambers J. 2009 The importance of niches for the maintenance of species diversity. *Nature* **461**, 254-257. (doi:10.1038/nature08251)

[9] Siepielski A, McPeek M. 2010 On the evidence for species coexistence: A critique of the coexistence programme. *Ecology* **91**, 3153-3164. (doi:10.1890/10-0154.1)

[10] Grave D, Canham CD, Beaudet M, Messier C. 2006 Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett.* **9**, 399-409. (doi:10.1111/j.1461-0248.2006.00884.x)

[11] Zhou SR, Zhang DY. 2008 A nearly neutral model of biodiversity. *Ecology* **89**, 248-258. (doi:10.1890/06-1817.1)

[12] Gilpin ME. 1975 Limit cycles in competition communities. *Am. Nat.* **109**, 51-60. (doi:10.1086/282973)

[13] May RM, Leonard WJ. 1975 Nonlinear aspects of competition between three species. *SIAMJ. Appl. Math.* **29**, 243-253. (doi:10.1137/0129022)

[14] Tilman D. 1994 Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2-16. (doi:10.2307/1939377)

[15] Huisman J, Weissing FJ. 1999 Biodiversity of plankton by species oscillations and chaos. *Nature* **402**, 407-410. (doi:10.1038/46540)

[16] Kerr B, Riley MA, Feldman MW, Bohannan BJM. 2002 Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* **418**, 171-174. (doi:10.1038/nature00823)

[17] Laird RA, Schamp BS. 2006 Competitive intransitivity promotes species coexistence. *Am. Nat.* **168**, 182-193. (doi:10.1086/506259)

[18] Laird RA, Schamp BS. 2008 Does local competition increase the coexistence of species in intransitive networks? *Ecology* **89**, 237-247. (doi:10.1890/07-0117.1)

[19] Allesina S, Levine JM. 2011 A competitive network theory of species diversity. *PNAS* **108**, 5638-5642. (doi:10.1073/pnas.1014428108)

[20] Rojas-Echenique JR, Allesina S. 2011 Interaction rules affect species coexistence in intransitive networks. *Ecology* **92**, 1174-1180. (doi:10.1890/10-0953.1)

[21] Soliveres S, *et al.* 2015 Intransitive competition is widespread in plant communities and maintains their species richness. *Ecol. Lett.* **18**, 790-798.

(doi:10.1111/ele.12456)

[22] Gallien L, Zimmermann NE, Levine JM, Adler PB, Wootton T. 2017 The effects of intransitive competition on coexistence. *Ecol. Lett.* **20**, 791-800. (doi:10.1111/ele.12775)

[23] Wootton T. 2001 Prediction in complex communities: analysis of empirically derived Markov models. *Ecology* **82**, 580-598. (doi:10.1890/0012-9658(2001)082[0580:PICCAO]2.0.CO;2)

[24] Cameron DD, White A, Antonovics J. 2009 Parasite–grass–forb interactions and rock–paper–scissor dynamics: predicting the effects of the parasitic plant *Rhinanthus minor* on host plant communities. *J. Ecol.* **97**, 1311-1319. (doi:10.1111/j.1365-2745.2009.01568.x)

[25] Stouffer DB, Wainwright CE, Flanagan T, Mayfield, MM. 2018 Cyclic population dynamics and density-dependent intransitivity as pathways to coexistence between co-occurring annual plants. *J. Ecol*. **106**, 838-851. (doi:10.1111/1365-2745.12960)

[26] Soliveres S, Lehmann A, Boch S, *et al.* 2018 Intransitive competition is common across five major taxonomic groups and is driven by productivity, competitive rank and functional traits. *J. Ecol*. **106**, 852-864. (doi:10.1111/1365-2745.12959)

[27] Ulrich W, Kubota Y, Piernik A, Gotelli NJ. 2018 Functional traits and environmental characteristics drive the degree of competitive intransitivity in European saltmarsh plant communities. *J. Ecol*. **106**, 865-876. (doi:10.1111/1365-2745.12958)

[28] Abrams P. 1983 The theory of limiting similarity. *Annu. Rev. Ecol. Syst.* **14**, 359-376. (doi:10.1146/annurev.es.14.110183.002043)

[29] Wootton JT. 2002 Indirect effects in complex ecosystems: recent progress and future challenges. *J. Sea Res.* **48**, 157-172. (doi:10.1016/s1385-1101(02)00149-1)

[30] Wootton JT. 1994 The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.* **25**, 443-466. (doi:10.1146/annurev.es.25.110194.002303)

[31] Werner EE, Peacor SD. 2003 A review of trait-mediated indirect interactions in

ecological communities. *Ecology* **84**, 1083-1100. (doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2)

[32] Poisot T, Stouffer DB, Gravel D. 2015 Beyond species: why ecological interaction networks vary through space and time. *Oikos* **124**, 243-251. (doi:10.1111/oik.01719)

[33] Bairey E, Kelsic ED, Kishony R. 2016 High-order species interactions shape ecosystem diversity. *Nat. Commun.* **7**, 12285. (doi:10.1038/ncomms12285)

[34] Grilli J, Barabás G, Michalska-Smith MJ, Allesina S. 2017 Higher-order interactions stabilize dynamics in competitive network models. *Nature* **548**, 210. (doi:10.1038/nature23273)

[35] Levine JM, Bascompte J, Adler PB, Allesina S. 2017 Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* **546**, 56-64. (doi:10.1038/nature22898)

[36] Letten AD, Stouffer DB. 2019 The mechanistic basis for higher-order interactions and non-additivity in competitive communities. *Ecol. Lett.* **22**, 423-436. (doi:10.1111/ele.13211)

[37] Mayfield MM, Stouffer DB. 2017 Higher-order interactions capture unexplained complexity in diverse communities. *Nature Ecol. Evol.* **1**, 62. (doi:10.1038/s41559-016-0062)

[38] Hastings A. 1980 Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.* **18**, 363-373. (doi:10.1016/0040-5809(80)90059-3)

[39] Nee S, May RM. 1992 Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Animal Ecol.* **61**, 37-40. (doi:10.2307/5506)

[40] Levins R. 1969 Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entmol. Soc. Am.* **15**, 237-240. (doi:10.1093/besa/15.3.237)

[41] MacArthur RH, Wilson EO. 1967 The theory of island biogeography. *Monographs in Population Biology*. Princeton University Press, Princeton, New Jersey.

[42] Leibold MA. 1995 The niche concept revisited: mechanistic models and

community context. *Ecology* **76**, 1371-1382. (doi:10.2307/1938141)

[43] Paine RT. 1984 Ecological determinism in the competition for space: the Robert H. MacArthur Award Lecture. *Ecology* **65**, 1339-1348. (doi:10.2307/1939114)

[44] McCoy SJ, Pfister CA. 2014 Historical comparisons reveal altered competitive interactions in a guild of crustose coralline algae. *Ecol. Lett.* **17**, 475-483. (doi:10.1111/ele.12247)

[45] Barabás G, D'Andrea R, Stump SM. 2018 Chesson's coexistence theory. *Ecol. Monogr.* **88**, 277-303. (doi:10.1002/ecm.1302)

[46] Chen D, Liao J, Bearup D, Li Z. 2020 Habitat heterogeneity mediates effects of individual variation on spatial species coexistence. *Proc. R. Soc. B* **287**, 20192436. (doi:10.1098/rspb.2019.2436)

[47] Wilson DS. 1992 Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* **73**, 1984-2000. (doi:10.2307/1941449)

[48] Tekin E, *et al.* 2018 Prevalence and patterns of higher-order drug interactions in *Escherichia coli*. *NPJ Syst. Biol. Appl.* **4**, 31. (doi:10.1038/s41540-018-0069-9)

[49] Worthen WB, Moore JL. 1991 Higher-order interactions and indirect effects: a resolution using laboratory drosophila communities. *Am. Nat.* **138**, 1092-1104. (doi:10.2307/2462509)

[50] Pacala SW, Tilman D. 1993 Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.* **143**, 222-257. (doi:10.2307/2462642)

[51] Hart SP, Schreiber SJ, Levine JM. 2016 How variation between individuals affects species coexistence. *Ecol. Lett.* **19**, 825-838. (doi:10.1111/ele.12618)

[52] Hart SP, Usinowicz J, Levine JM. 2017 The spatial scales of species coexistence. *Nat. Ecol. Evol.* **1**, 1066-1073. (doi:10.1038/s41559-017-0230-7)

[53] Uriarte M, Menge D. 2018 Variation between individuals fosters regional species coexistence. *Ecol. Lett.* **21**, 1496-1504. (doi:10.1111/ele.13130)

[54] Czárán TL, Hoekstra RF, Pagie L. 2002 Chemical warfare between microbes promotes biodiversity. *PNAS* **99**, 786-790. (doi:10.1073/pnas.012399899)

Figure legends

Figure 1. Effect of variation in competition strength on the fraction of surviving species (solid line plus shaded area: mean ± SDs of 20 replicates for each case) under both pairwise (red) and higher-order (blue) competition in a multispecies system (n=50) subject to habitat loss (U=0, 0.25, 0.5 and 0.75) at steady state, by considering both variation in vital rates (I-IV: colonization rates $c_i \sim unif[0.6, 1]$ & mortality rates $e_i \sim unif[0, 0.2]$) and identical vital rates (V-VIII: c=0.8 & e=0.1). Each matrix H is randomly generated using the given two elements {0.5, 0.5}, {0.49, 0.51}, {0.48, 0.52} …{0, 1} respectively with 0.01 increments around the mean $\bar{H}$=0.5 (note $H_{ij}+H_{ji}=1$), and the corresponding values of relative intransitivity (RI) are shown in figure S8 in *Appendix B* (electronic supplementary material). Variation in competition strength is represented by the coefficient of variation $C.V.(H) = \sigma_H/\bar{H}$ with σ_H being the standard deviation for all elements H_{ij} and $\bar{H}$ (=0.5) the mean of these elements. Note that, only one species can survive in graphs (V-VIII) when there is no variation in competition strength in the systems incorporating a continuous stochastic environmental perturbation $W_i(t) = \Omega \times [1 - 2 \cdot \delta(t)] \cdot p_i(t)$, with $\Omega = 0.1$ being the perturbation size, $\delta(t) \sim unif[0, 1]$ a uniform random variate that varies temporally, and $p_i(t)$ the site occupancy of species i at time t (see *Methods*).

Figure 2. Effect of relative intransitivity (RI) on species coexistence in a multispecies (n=50) system subject to habitat loss (U=0, 0.25, 0.5 and 0.75), regarding variation in vital rates (I-IV: $c_i \sim unif[0.6, 1]$ & $e_i \sim unif[0, 0.2]$) and identical vital rates (V-VIII: c=0.8 & e=0.1)

separately. Two types of competition are considered: pairwise (red circles) and higher-order (blue circles) competition, with 3-order polynomial fitting (solid lines, measured by R^2). A broad range of *RI* values are generated randomly with 20 replicates for each perturbed fraction f (=0, 0.05, 0.1…, 0.95, 1), using elements H_{ij}=0 or 1 in the tournament matrix H (note $H_{ij} + H_{ji}$=1; see *Methods*).

Figure 3. Effect of habitat loss on the fraction of surviving species (20 replicates for each case) in a multispecies competitive system (n=50) with variation in vital rates ($c_i \sim unif[0.6, 1]$ & $e_i \sim unif[0, 0.2]$), fitted by 3-degree polynomial functions (solid lines, measured by R^2). Three levels of relative intransitivity (*RI*) are considered for both pairwise (red circles) and higher-order (blue circles) competition, with H_{ij}=0 or 1 in the tournament matrix H (note $H_{ij} + H_{ji}$=1; see *Methods*): (a) $0.55<RI<0.6$, (b) $0.75<RI<0.8$ and (c) $0.9<RI<0.95$ (i.e. randomly-structured interactions).

Figure 4. Effect of initial species richness on the fraction of surviving species in a competitive system subject to habitat loss (U=0, 0.25, 0.5 and 0.75) at steady state, considering both variation in vital rates (I-IV: $c_i \sim unif[0.6, 1]$ & $e_i \sim unif[0, 0.2]$) and identical vital rates (V-VIII: c=0.8 & e=0.1) at $0.9<RI<0.95$ (with H_{ij}=0 or 1 in the tournament matrix H: $H_{ij} + H_{ji}$=1; see *Methods*). Each case is run with 20 replicates for pairwise (red circles) and higher-order (blue circles) competition separately with linear fitting (but with the x-axis log scale; solid lines), measured by R^2.

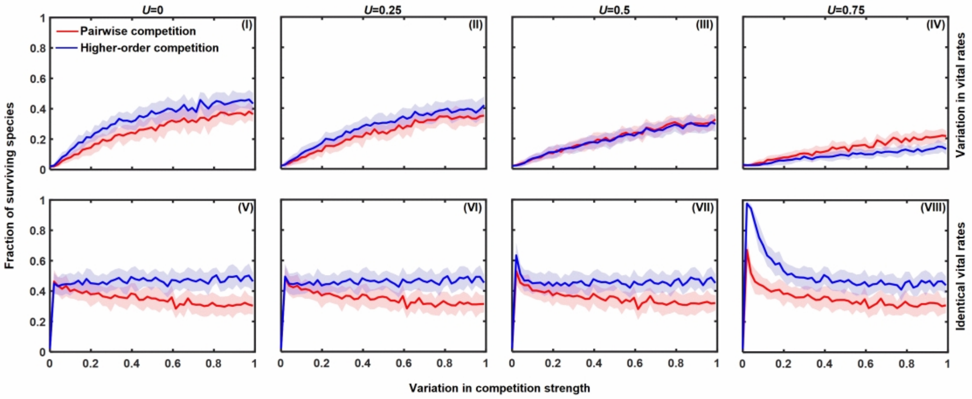

Figure 1. Effect of variation in competition strength on the fraction of surviving species (solid line plus shaded area: mean ± SDs of 20 replicates for each case) under both pairwise (red) and higher-order (blue) competition in a multispecies system (n=50) subject to habitat loss (U=0, 0.25, 0.5 and 0.75) at steady state, by considering both variation in vital rates (I-IV: colonization rates ci~unif[0.6, 1] & mortality rates ei~unif[0, 0.2]) and identical vital rates (V-VIII: c=0.8 & e=0.1). Each matrix H is randomly generated using the given two elements {0.5, 0.5}, {0.49, 0.51}, {0.48, 0.52} …{0, 1} respectively with 0.01 increments around the mean H =0.5 (note Hij+Hji=1), and the corresponding values of relative intransitivity (RI) are shown in figure S8 in Appendix B (electronic supplementary material). Variation in competition strength is represented by the coefficient of variation C.V.(H)=σ_H/H with σ_H being the standard deviation for all elements H_ij and H (=0.5) the mean of these elements. Note that, only one species can survive in graphs (V-VIII) when there is no variation in competition strength in the systems incorporating a continuous stochastic environmental perturbation W_i (t)=Ω×[1-2·δ(t)]·p_i (t), with Ω=0.1 being the perturbation size, δ(t)~unif[0,1] a uniform random variate that varies temporally, and p_i (t) the site occupancy of species i at time t (see Methods).

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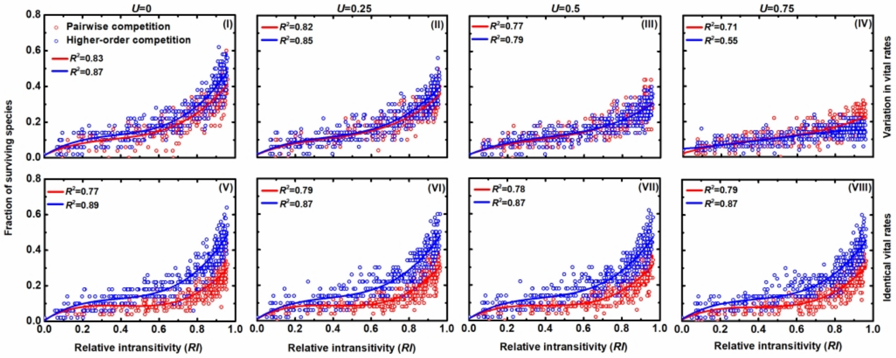

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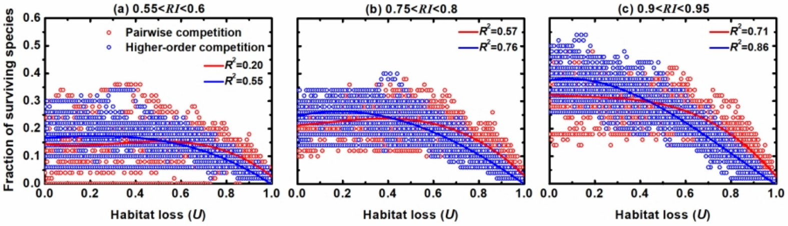

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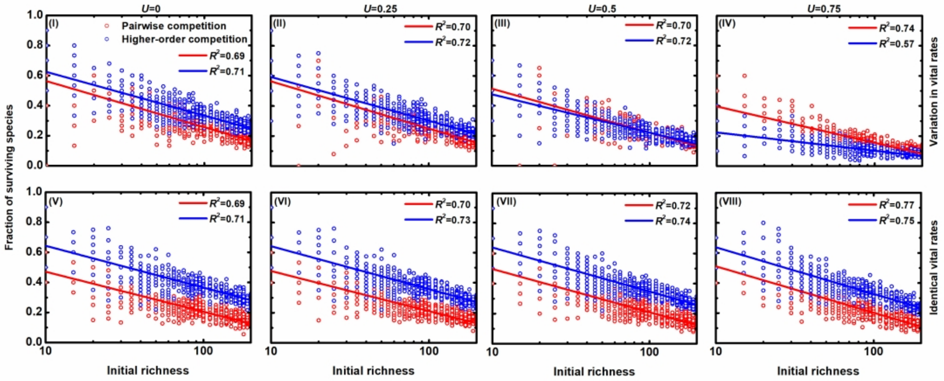

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