

## Interaction rules affect species coexistence in intransitive networks

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**Abstract.** Intransitive communities, those in which species' abilities cannot be ranked in a hierarchy, have been the focus of theoretical and empirical research, as intransitivity could help explain the maintenance of biodiversity. Here we show that models for intransitive competition embedding slightly different interaction rules can produce opposite patterns. In particular, we find that interactions in which an individual can be outcompeted by its neighbors, but cannot outcompete its neighbors, produce negative frequency dependence that, in turn, promotes coexistence. Whenever the interaction rule is modified toward symmetry (the individual and the neighbors can outcompete each other) the negative frequency dependence vanishes, producing different coexistence levels. Macroscopically, we find that asymmetric interactions yield highest biodiversity if species compete globally, while symmetric interactions favor highest biodiversity if competition takes place locally.

*Key words:* biodiversity; coexistence; competition; intransitivity; network; tournament.

### INTRODUCTION

Competitive intransitivity is the situation in which the competitive abilities of species cannot be ranked in a perfect hierarchy. The most common case of intransitivity is the so-called rock–paper–scissors configuration in which a species A displaces species B, B displaces C, and C displaces A (Gilpin 1975, May and Leonard 1975). Because this type of configuration can prevent the emergence of a competitive dominant, intransitivity is a mechanism that could play a key role in the maintenance of biodiversity (Buss and Jackson 1979, Huisman and Weissing 1999, Frea and Abraham 2001, Huisman et al. 2001, Kerr et al. 2002, Kirkup and Riley 2004, Laird and Schamp 2006, Reichenbach et al. 2007, Laird and Schamp 2008, 2009).

In addition to theoretical interest in the subject, empirical evidence of intransitive competition has been provided for coral reef communities, plants, lizards, and bacterial communities (Buss and Jackson 1979, Taylor and Aarssen 1990, Sinervo and Lively 1996, Kerr et al. 2002, Kirkup and Riley 2004). Quantifying the frequency of this type of mechanism in nature is of great interest, and some researchers have argued that intransitivity should be widespread (Sinervo and Calsbeek 2006).

In a recent article, Laird and Schamp (2008) showed how intransitive interactions based on local competition

(i.e., when each individual can interact only with its nearest neighbors) lead to lower species richness than intransitive interactions with global competition (i.e., where neighbors are sampled at random from the whole landscape). This is a surprising result, given that several theoretical and experimental arguments have predicted exactly the opposite: local competition should improve species coexistence through the formation of “shifting patches” and other mechanisms (Kerr et al. 2002, Laird and Schamp 2006, 2008, 2009, Reichenbach et al. 2007).

Here we show that the opposite patterns of coexistence are caused by slight changes in the “interaction rules” that model competition among individuals: depending on the details of the interaction rule, global competition can increase or decrease the coexistence level with respect to the local case.

In particular, we find that the introduction of a “focal individual” interacting with several neighbors produces negative frequency dependence, increasing the probability of rescuing species close to extinction and depressing the density of dominant species. When instead there is no “focal individual,” simulations yield a lower observed level of coexistence for the global setting. To illustrate this, we calculate the expected growth rate of a species, at different densities, for the global competition setting, with and without focal individuals. We then argue that the effects of local competition result from patch formation as (1) the “effective size” of dominant species is reduced and that of rare species is increased, yielding a lower level of frequency dependence and (2) slower

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dynamics reduce the probability of observing stochastic extinctions.

Given the sensitivity of the pattern to changes in the interaction rules, great attention should be put in the justification of assumptions, and experiments should be performed to investigate how species behave in nature.

## METHODS

### *Competition tournaments*

The competitive relationships among  $n$  species with similar physiological and ecological traits can be described by a tournament. We define a tournament  $\mathbf{T}$  as a matrix (or network) in which we have  $\mathbf{T}_{ij} = 1$  (or in the network  $i \rightarrow j$ ) whenever  $j$  outcompetes  $i$ , and  $\mathbf{T}_{ij} = 0$  otherwise (Laird and Schamp 2006, 2008, 2009). Because there are  $\binom{n}{2}$  pairs of species, the matrix will contain exactly  $\binom{n}{2}$  ones.

### *Simulations*

We perform simulations similar to those of Laird and Schamp (2008): (1) we have a  $100 \times 100$  square lattice with periodic boundaries; (2) we populate the lattice with individuals drawn randomly from  $n$  species; (3) a tournament describing the competitive relationships among the species is generated by a probabilistic algorithm (Appendix B); (4) at each time step, we perform a “competition event” using the “interaction rule” specified below; (5) we repeat step 3 for 500 generations ( $5 \times 10^6$  steps); (6) we record the number of extant species at the end of the simulation. As a caveat, note that the small size of the lattice and the relatively short simulation could preclude the formation of self-organizing patterns (Szabó et al. 2007) and the reaching of a stationary distribution. However, in order to faithfully replicate the results obtained by Laird and Schamp (2008), we used the same parameters.

As in Laird and Schamp (2008), we record, for each simulation, a “relative intransitivity index” (RI; Appendix A) that expresses how intransitive a tournament is. We then correlate this index with the number of extant species at the end of the simulation.

### *Two possible “interaction rules”*

We describe here two possible “interaction rules”: one is the rule used by Laird and Schamp (2008) and the other is an alternative, more symmetrical rule. For each interaction rule, we have two settings: local and global.

Laird and Schamp (2008) used the following: (1) at each step we sample a “focal individual” at random. (2a) In the local setting, we check if any of the eight nearest neighbors can outcompete the focal individual. If only one of the neighbors is a superior competitor, then it substitutes the focal individual. If more than one neighbor is a superior competitor, one is randomly chosen to substitute the focal individual. Otherwise the focal individual remains unaltered. (2b) In the global

setting, instead of using the eight nearest neighbors, we sample eight individuals at random from the whole lattice and use them as neighbors. The rest is the same.

An alternative interaction rule is the following: (1a) in the local setting, we sample two adjacent individuals at random; (1b) in the global setting, we sample two individuals at random; (2) if one of the two individuals can outcompete the other, it substitutes it. One advantage of the second rule is that its dynamics, in the global setting, can be approximated by simple mean field models based on differential equations. The dynamics of the rule with a focal individual, on the other hand, would be harder to model given that there could be neighborhood size effects.

## RESULTS

### *Long-term coexistence and relative intransitivity*

We repeated the simulations described in Laird and Schamp (2008), where competition happens between a focal individual and eight neighbors. We contrast these results with those obtained when there is no focal individual.

Moreover, in the interaction rules of Laird and Schamp (2008), we vary the number of neighbors with which the focal individual interacts during a competition event, exploring the effects of having one, two, three, four, or eight neighbors on global and local settings.

For each interaction rule, we ran 500 replicates. To sample tournaments with a broad spectrum of RI, we generated the tournaments using an algorithm described in Appendix B.

Fig. 1 summarizes the mean number of coexisting species after 500 generations, for the interaction rule with eight neighbors and a focal individual, and for the symmetric interaction rule. As expected, in case of a focal individual, global competition produced higher species richness than local competition. Without a focal individual, however, the result is reversed: local competition produces higher species richness than global competition. In all cases, the relative intransitivity index is positively correlated with the fraction of extant species. Also, the slopes of the various lines differ, signaling an interaction between the type of rule used and intransitivity (Laird and Schamp 2008).

We also found that as the number of neighbors with which the focal species can interact decreases, so does the mean number of coexisting species: the effect on coexistence is positively correlated with the number of neighbors (data not shown). Global competition leads to higher coexistence than local competition in every case, except the one-neighbor case.

### *Effects of having a focal species*

In the interaction rules using focal individuals (Laird and Schamp 2008), a focal individual is randomly chosen to compete with eight individuals in its neigh-

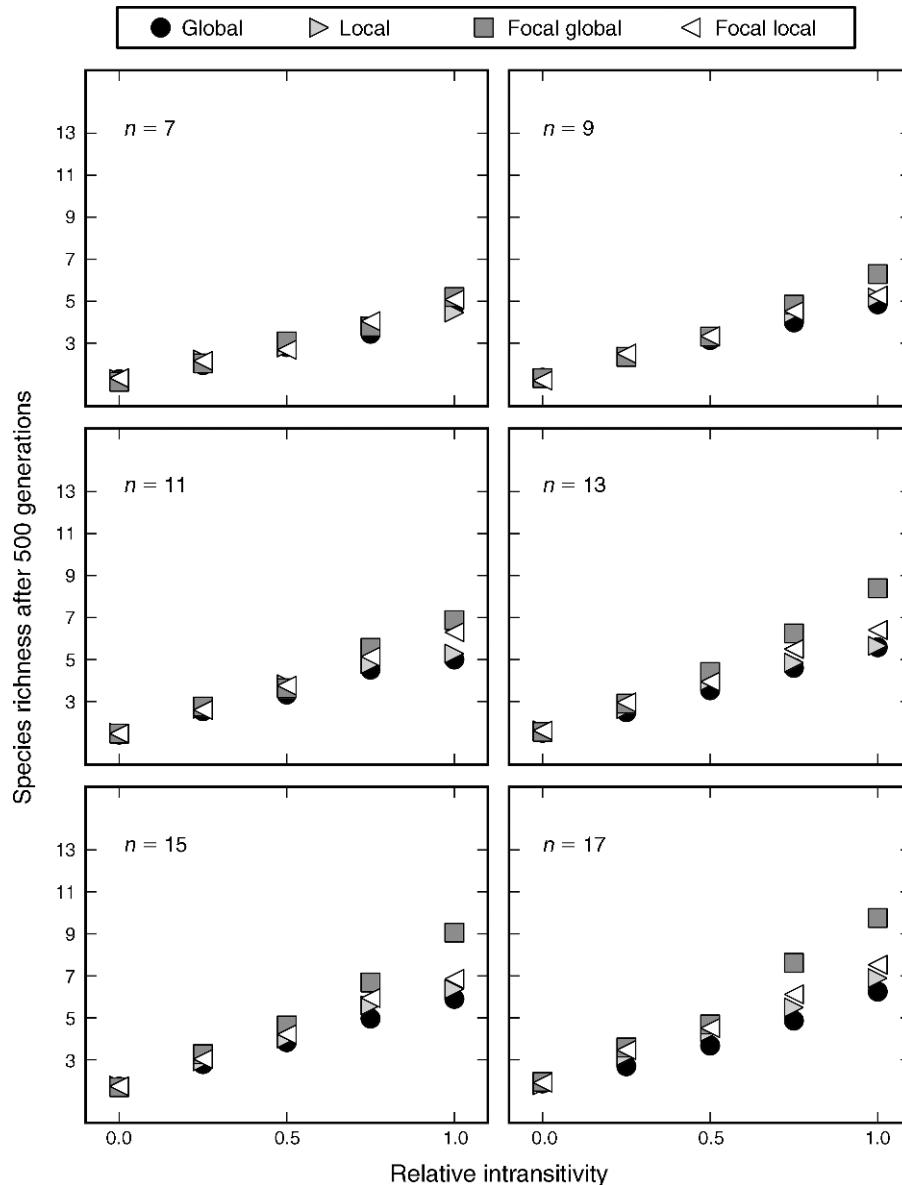


FIG. 1. Mean number of coexisting species after 500 simulation generations ( $y$ -axis), as a function of initial species richness (different  $n$  for each panel), relative intransitivity ( $x$ -axis), and interaction rule.

neighborhood. If any of these neighbors are better competitors, the focal individual is replaced by a randomly chosen superior neighbor, otherwise it remains unchanged. Therefore, during one competition event, the density of the species of the focal individual can never increase, it can only decrease or stay the same.

To show the effects of having a focal species, we take the simplest possible case that can illustrate our findings. Suppose that we have three species in a “rock–paper–scissors” configuration: A outcompetes B, B outcompetes C, and C outcompetes A.

To simplify the computation, we analyze the global setting. There are  $K$  cells in the lattice, and  $Y$  are of species A. The density of A is  $y = Y/K$ , while those of B and C are  $(1 - y)/2 = (K - Y)/2K$ .

This case, where B and C have equal densities, is particularly simple because using the symmetric rule, the expected growth of A is exactly 0: for each sample in which A and B interact (leading to an increase in the density of A) we can find, with the same probability, an interaction between C and A (leading to a decrease in the density of A). Although we analyze the case in which

TABLE 1. Effect of interaction on species A for a “rock–paper–scissors” tournament with a focal individual and one neighbor, when A has density  $y = Y/K$  while B and C have the same density  $(1 - y)/2 = (K - Y)/2$ .

Focal	Neighbor	Effect on A	$p$	$\hat{p}$
B	A	+1	$\frac{K - Y}{2K} \frac{Y}{K - 1}$	$\frac{1 - y}{2} y$
A	C	-1	$\frac{Y}{K} \frac{Y - K}{2(K - 1)}$	$y \frac{1 - y}{2}$

Notes: We list all the interactions that can affect the density of A, their exact ( $p$ ), and approximate ( $\hat{p}$ ) probabilities of occurrence for the global setting. Results are for the Laird and Schamp (2008) interaction rule with a focal individual and one neighbor. The expected growth of A is 0.

B and C have the same densities in order to keep the computation simple, the derivation can be generalized to cases in which the densities of the species are different.

To begin with, let us suppose that the neighborhood size is one instead of eight: at each time step, we pick a focal individual and a neighbor. If the neighbor outcompetes the focal, it substitutes it. In Table 1 we list all the possible cases in which the density of A can be altered, and we compute the expected growth of A. For each possible combination that can alter the density of A, we report the exact probability ( $p$ ), an approximate probability for  $K \gg 1$  ( $\hat{p}$ ), and the effect that the

configuration would have on the density of A. In the case of one neighbor, whenever the other two species have the same density, the expected growth of A is 0 (as it was with the symmetric rule).

The situation becomes more interesting when the number of neighbors increases. In a two-neighbor setting, at each time step we sample a focal individual and two neighbors. If any of the neighbors can outcompete the focal species, it substitutes it. In Table 2 we list all the possible configurations in which the density of A could be altered. Note that the expected growth of A is no longer 0. Rather, it depends on the density of A. When A is rare,

TABLE 2. Effect of interaction on species A for a “rock–paper–scissors” tournament with a focal individual and two neighbors, when A has density  $y = Y/K$  while B and C have the same density  $(1 - y)/2 = (K - Y)/2$ .

Focal	Neighbor 1	Neighbor 2	Effect on A	$p$	$\hat{p}$
B	A	A	+1	$\frac{Y(Y - 1)(K - Y)}{2K(K - 1)(K - 2)}$	$y^2 \frac{1 - y}{2}$
B	A	B	+1	$\frac{Y(K - Y)(K - Y - 2)}{4K(K - 1)(K - 2)}$	$y \frac{(1 - y)^2}{4}$
B	B	A	+1	$\frac{Y(K - Y)(K - Y - 2)}{4K(K - 1)(K - 2)}$	$y \frac{(1 - y)^2}{4}$
B	A	C	+1	$\frac{Y(K - Y)^2}{4K(K - 1)(K - 2)}$	$y \frac{(1 - y)^2}{4}$
B	C	A	+1	$\frac{Y(K - Y)^2}{4K(K - 1)(K - 2)}$	$y \frac{(1 - y)^2}{4}$
A	A	C	-1	$\frac{Y(Y - 1)(K - Y)}{2K(K - 1)(K - 2)}$	$y^2 \frac{1 - y}{2}$
A	C	A	-1	$\frac{Y(Y - 1)(K - Y)}{2K(K - 1)(K - 2)}$	$y^2 \frac{1 - y}{2}$
A	C	C	-1	$\frac{Y(K - Y)(K - Y - 2)}{4K(K - 1)(K - 2)}$	$y \frac{(1 - y)^2}{4}$
A	B	C	-1	$\frac{Y(K - Y)^2}{4K(K - 1)(K - 2)}$	$y \frac{(1 - y)^2}{4}$
A	C	B	-1	$\frac{Y(K - Y)^2}{4K(K - 1)(K - 2)}$	$y \frac{(1 - y)^2}{4}$

Notes: We list all the interactions that can affect the density of A, as well as their exact ( $p$ ) and approximate ( $\hat{p}$ ) probabilities of occurrence for the global setting. Results are for the Laird and Schamp (2008) interaction rule with a focal individual and two neighbors. The expected growth of A is  $Y(K - Y)(K - 3Y)/4K(K - 1)(K - 2)$ . The approximate growth of A is  $y(1 - y)(1 - 3y)/4$ .

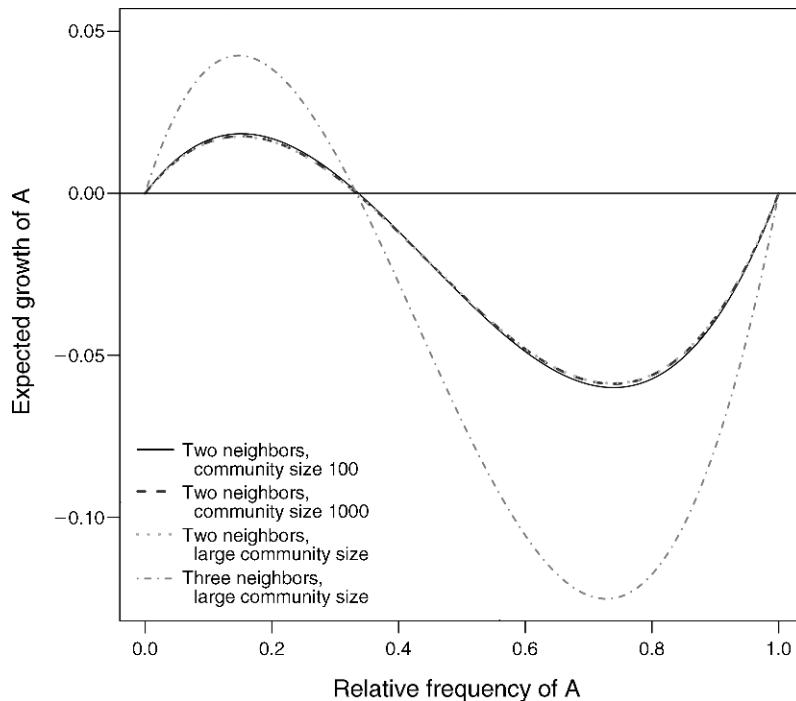


FIG. 2. Expected growth rate for species A in a rock–paper–scissors tournament as a function of the frequency of A. Analytic results for the global setting with a focal individual. Key to line types: solid, two neighbors, community size 100; dashed, two neighbors, community size 1000; dotted, two neighbors, large community size; dot-dashed, three neighbors, large community size. Note that the “large size approximation” line (dotted) lies almost directly on top of the “exact community size 1000” line (solid). Both the symmetric rule and the one-neighbor focal rule predict a growth rate of 0 independently of the density of A.

the expected growth is positive; when all species are equally represented, the expected growth is 0; and when A is dominant, the expected growth is negative. This is commonly known as negative frequency dependence. In Fig. 2 we show the expected growth of A as a function of its relative density for small communities ( $K = 100$ ) and large communities ( $K = 1000$ ). We also show an approximation of the growth of A (assuming  $K \gg 1$ ). We note that for large  $K$  the approximate growth of A closely matches the exact result.

What happens when three neighbors are present? The number of possible combinations that affect the growth of A grows considerably (Appendix C), but it is still possible to compute the expected growth. In Fig. 2, we show that the negative frequency dependence is enhanced by an increase in the number of neighbors.

In Fig. 3 we show the approximate growth of A as a function of the relative densities of all three species. When A is relatively rare (near the edge opposite the point labeled A), its growth rate is higher with a two-neighbor interaction rule than with a one-neighbor rule for any combination of B and C. The opposite is true when A is common. Again, the effect is enhanced with a three-neighbor interaction rule (Appendix C). Another effect of the “focal individual” rule is a general decrease

in the speed of dynamics (i.e., frequency of “substitution events”). This effect is discussed in Appendix D.

To summarize the results obtained so far, we find negative frequency dependence whenever we use the focal individual rule and more than one neighbor. The effect is increased for a larger number of neighbors. In the absence of a focal individual, the effect disappears. This follows from the fact that whenever a species is rare, it is much more probable to sample one individual of this species as a neighbor of an inferior competitor than to find it as the focal individual with a superior competitor neighbor. The effect is enhanced when the neighborhood is expanded. As a limiting case, imagine we pick  $K - 1$  neighbors: in this case whenever the focal individual belongs to B, then the density of A is increased. The density of A is decreased only when an individual belonging to A is the focal one, which is much less probable when A is rare and B common.

#### *Effects of local interactions*

Whenever we have local interactions, we observe the formation of patches with common species forming larger patches. Because of these patches, the only “active” individuals (i.e., those that can change state) are those on the boundaries between patches. This

decreases the role of frequency dependence, because the number of individuals on the boundary will make the “effective density” of each species more uniform. For example, imagine we have circular patches. Then, when we have approximately  $\pi r^2$  individuals inside a patch, where  $r$  is the radius of a particular patch. Of these, approximately  $2\pi r$  are on the circumference. Therefore, rare species (which have smaller  $r$ ) will have proportionally more individuals on the circumference than common species (which have larger  $r$ ).

The negative frequency dependence illustrated above is based on the asymmetry in probability: sampling an individual belonging to a rare species as a neighbor of a lesser focal individual is much more probable than as the focal individual with a superior neighbor. Clearly, when we have patches these two probabilities become closer, reducing the effect of frequency dependence. We believe this to be the cause of the pattern observed by Laird and Schamp (2008).

Note also that local spatial structure (especially patch formation) is going to reduce the effects of (positive or negative) frequency dependence by altering the “friction surface” in which individuals can change state. Other mechanisms, such as dispersal limitation and mobility (Reichenbach et al. 2007) are likely to alter frequency dependence. The interplay of these factors should be researched further.

#### DISCUSSION

Our results confirm that intransitive competition enhances biodiversity, consistent with many earlier findings (Buss and Jackson 1979, Huisman and Weissing 1999, Huisman et al. 2001, Kerr et al. 2002, Laird and Schamp 2008, 2009). However, we have shown that slight changes in the way competitors interact can reverse how global vs. local competition modify these biodiversity patterns. Therefore, particular attention should be devoted to testing, theoretically and experimentally, which mode of interaction is more appropriate for modeling a given community.

Symmetric interaction rules, like the one used here, are mathematically simpler but may not always be appropriate. In communities where competition is more diffuse than direct, an interaction rule with a focal individual and multiple neighbors would be more appropriate. Take for example forest dynamics. When the death of a tree creates a gap in the canopy, seedlings from the seed bank compete to fill the gap. Under these conditions, known as gap dynamics, a “focal individual” dies, and the competition regards its neighborhood. Models should therefore favor a “focal individual” rule with interactions that are either local (if the seed bank results from dispersal-limited processes) or global (if the dispersal kernel is wide). On the other hand, when individuals compete for space and can grow over each other (a typical case could be lichens growing on rocks,

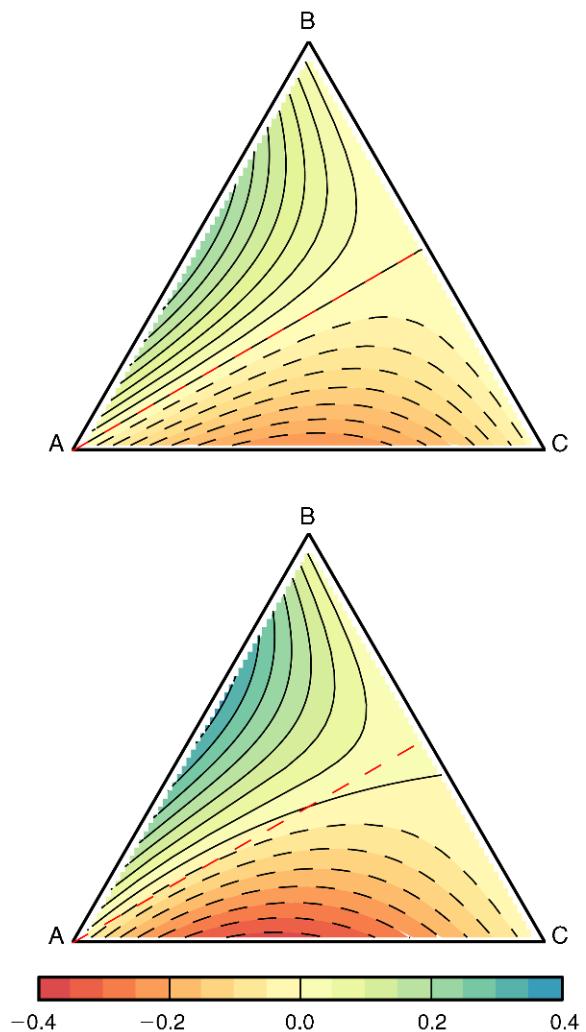


FIG. 3. Expected growth rate of species A in a three-species community when it competes with one neighbor (top), and two neighbors (bottom); as a function of the possible densities of the three species. Note that the dashed red lines correspond to the space in Fig. 2, where B and C have equal densities.

or corals and sponges on coral reef), a symmetric (and local) rule would be more appropriate.

Interaction rules with global competition are easier to analyze but will not adequately model systems where spatial structure is important. When interactions are spatially organized, local interaction rules are more appropriate. This is especially important because there is evidence (Durrett and Levin 1997, Szabó et al. 2007) that the self organizing patterns which develop in local competition models have a role in maintaining diversity. For example, Kerr et al. (2002) found that allowing spatial structure (by growing the bacteria on a Petri dish rather than a mixed flask) made the difference between

coexistence and monoculture for a three strain community of *E. coli*.

We also provided a different explanation for the patterns observed by Laird and Schamp (2008): we have shown how the presence of a focal individual causes a strong negative frequency dependence in the global setting, while in the local setting this effect is dampened. To further illustrate this point, we have contrasted the results with those obtained using a more symmetric interaction rule. Finally, we showed how the pattern observed by Laird and Schamp (2008) strongly depends on the number of neighbors.

As it happens, in many ecological models, the devil is in the details. The only exorcism available to theoretical ecologists is a careful examination of the models' assumptions and a detailed analysis of their consequences.

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#### APPENDIX A

An analytical method used to efficiently calculate a tournament's "relative intransitivity index" (RI) (*Ecological Archives* E092-096-A1).

#### APPENDIX B

Description of the algorithm used to generate tournaments with an even distribution of relative intransitivity indices (*Ecological Archives* E092-096-A2).

#### APPENDIX C

A table and a figure showing the expected growth of species A with one focal species and three neighbors (*Ecological Archives* E092-096-A3).

#### APPENDIX D

A discussion on the role that the speed of dynamics has on observed patterns of coexistence (*Ecological Archives* E092-096-A4).