

## DOES LOCAL COMPETITION INCREASE THE COEXISTENCE OF SPECIES IN INTRANSITIVE NETWORKS?

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**Abstract.** Competitive intransitivity, a situation in which species' competitive ranks cannot be listed in a strict hierarchy, promotes species coexistence through "enemy's enemy indirect facilitation." Theory suggests that intransitivity-mediated coexistence is enhanced when competitive interactions occur at local spatial scales, although this hypothesis has not been thoroughly tested. Here, we use a lattice model to investigate the effect of local vs. global competition on intransitivity-mediated coexistence across a range of species richness values and levels of intransitivity. Our simulations show that local competition can enhance intransitivity-mediated coexistence in the short term, yet hinder it in the long term, when compared to global competition. This occurs because local competition slows species disaggregation, allowing weaker competitors to persist longer in the shifting spatial refuges of intransitive networks, enhancing short-term coexistence. Conversely, our simulations show that, in the long term, local competition traps disaggregated species in unfavorable areas of the competitive arena, where they are excluded by superior competitors. As a result, in the long term, global intransitive competition allows a greater number of species to coexist than local intransitive competition.

**Key words:** aggregation; biodiversity; cellular automaton; coexistence; competition; global competition; intransitivity; lattice model; local competition; species coexistence.

### INTRODUCTION

A major goal in ecology is to reconcile the competitive exclusion principle with the fact that, in many communities, more species coexist than can seemingly be accounted for by the number of limiting resources. Many factors thought to promote coexistence are extrinsic to the competitive process and work by mitigating competition (e.g., disturbance, predation, habitat heterogeneity [Tokeshi 1999]). One possible mechanism for coexistence that is intrinsic to the competitive process is competitive intransitivity. Competition between multiple species can range from hierarchical to intransitive. Hierarchical competition occurs when species can be ranked unambiguously in order of their competitive abilities. For example, in a competitively hierarchical community in which no two species are competitively equivalent, for every instance in which species A outcompetes species B, A also outcompetes all the species outcompeted by B, while B outcompetes none of the species that outcompete A. Intransitive competition, therefore, occurs in communities for which this is not the case. Rather, competitively intransitive communities are characterized by the existence of at least one competitive loop, such as the

following intransitive species triplet: species A outcompetes B, which outcompetes C, which, in turn, outcompetes A ( $A > B > C > A$ ). Species A, B, and C are tied in their competitive ranks at the community scale; however, at the scale of the individual, intransitivity renders species' competitive ranks ambiguous: the three species are ranked C-A-B with respect to species A, but they are ranked A-B-C with respect to species B, and B-C-A with respect to species C.

Intransitive competition can emerge from a number of ecological scenarios (e.g., Gilpin 1975, Jackson and Buss 1975, May and Leonard 1975, Karlson and Buss 1984, Huisman and Weissing 1999, 2001*a, b*, Huisman et al. 2001, Szabó and Czárán 2001, Czárán et al. 2002, Kerr et al. 2002). Regardless of intransitivity's ecological origin, competitively intransitive communities are, in theory, more resistant to competitive exclusion compared to competitively hierarchical communities (e.g., Karlson 1981, Karlson and Jackson 1981, Karlson and Buss 1984, Durrett and Levin 1994, 1998, Kerr et al. 2002, Laird and Schamp 2006). This is because of "enemy's enemy indirect facilitation" (see Vandermeer 1980): continuing with the previous example, species A, B, and C all have an "enemy's enemy" (B, C, and A, respectively) that acts as an indirect facilitator (i.e., by outcompeting C, A, and B, respectively). Due to this enemy's enemy phenomenon, increasingly intransitive communities (e.g., those with a greater proportion of species triplets for which  $A > B > C > A$ ) tend to have more species protected from competitive exclusion, and

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therefore, enhanced coexistence (see Laird and Schamp 2006).

Intransitive competition has been identified among sessile marine organisms including bryozoans, ascidians, cnidarians, sponges, and coralline algae (Buss and Jackson 1979, Buss 1980, 1990, Jackson 1983), as well among terrestrial plant species (Taylor and Aarssen 1990, Shipley 1993), lizards (Sinervo and Lively 1996, Sinervo et al. 2007), and bacteria (Kerr et al. 2002). The general importance of intransitive competition in community dynamics has not yet been determined, in large part due to the barriers posed by experiments examining competition between all possible species pairs for a large number of species (but see Wootton 2001, Dunstan and Johnson 2005). The communities for which intransitive competition has been identified are largely characterized by sessile individuals and local interactions. While some evidence for hierarchical competition among phytoplankton species has been observed (Huisman et al. 1999, Passarge et al. 2006), other studies have observed trade-offs between competition for multiple nutrients (Tilman 1981, Sommer 1986, van Donk and Kilham 1990), which is one possible mechanism for intransitive competition. However, the degree to which “paradoxically” species-rich phytoplankton communities compete intransitively remains an important empirical question.

Some theoretical studies suggest that intransitivity-mediated species coexistence is indeed more likely when interactions occur at the local scale, rather than globally (e.g., Durrett and Levin 1997, 1998, Szabó and Czárán 2001, Czárán et al. 2002, Kerr et al. 2002, Szabó et al. 2004, Károlyi et al. 2005, Zhang et al. 2006). Local competition is defined here as the tendency for individuals to compete with members of their immediate neighborhood, while global competition occurs when individuals compete with members of the community independent of their spatial location (e.g., in well-mixed systems). The argument that local competition is important to intransitivity-mediated coexistence is founded on the premise that local competition leads to the spontaneous formation of shifting patches (i.e., aggregations) of species that outcompete competitive subordinates on the expanding edge of their patch while they are simultaneously outcompeted by competitive superiors on the shrinking edge of their patch (i.e., a “balanced chase” of temporary spatial refuges [Durrett and Levin 1998, Frean and Abraham 2001, Kerr et al. 2002, Károlyi et al. 2005, Zhang et al. 2006]). Conversely, this line of argument maintains that when competition is global, spatial refuges cannot develop, increasing the rate that subordinate species are excluded, especially as their competitive superiors become more abundant (Durrett and Levin 1997, Kerr et al. 2002, Szabó et al. 2004, Károlyi et al. 2005). Nevertheless, other studies report intransitivity-mediated coexistence even when competition plays out globally (e.g., Huisman and Weissing 1999, 2001a, b, Huisman et al. 2001).

In part, disagreement about the role of local vs. global competition in intransitivity-mediated coexistence stems from the fact that these studies typically do not consider the requisite minimum of four levels of “localness” of competition and intransitivity (local-intransitive, local-hierarchical, global-intransitive, and global-hierarchical) to establish whether, and how, they combine to affect coexistence. For example, while Kerr et al. (2002) examine local and global interactions of an intransitive three-species system, they do not discuss the comparable hierarchical case and therefore cannot eliminate the possibility that the observed species coexistence is simply due to the localness of competition (e.g., Miyazaki et al. 2006).

This paper aims to characterize the interactive effects of local competition and intransitivity on species coexistence across a wide range of species richness and intransitivity values. Our primary hypothesis is that intransitivity more strongly promotes coexistence when competitive interactions are local compared to when they are global. To test this hypothesis, we compare outcomes from a local competition model (i.e., a lattice-based cellular automaton) with those from an analogous global competition model in which spatial structure is omitted. The results show that local competition promotes intransitivity-mediated coexistence for one measure of coexistence (the number of model generations until the first extinction), but contrary to expectation, hinders intransitivity-mediated coexistence for another measure of coexistence (the number of species remaining at the end of 500 model generations).

## METHODS

### *Competitive-outcomes matrices and the “relative intransitivity” index*

Competitive-outcomes matrices describe the competitive relationships within all  $s(s-1)/2$  species pairs in a community of  $s$  species (e.g., Petraitis 1979, Laird and Schamp 2006; Fig. 1a, b). Here, we assume that the outcomes of competition between species pairs are strictly unidirectional and deterministic. Each position in a competitive-outcomes matrix is filled with either 0, 1, or  $-$  (i.e., a “blank”). A 1 means that the row species outcompetes the column species while a 0 means the opposite (“blanks” occur when the row equals the column). If species A out-competes species B, then species B is out-competed by species A; therefore, the matrix is anti-symmetrical about the leading diagonal (Laird and Schamp 2006).

Indices of intransitivity are useful for summarizing competitive-outcomes matrices. Here, we use the “relative intransitivity” index. Relative intransitivity is equal to one minus the “relative variance” index of Laird and Schamp (2006):

$$\text{relative intransitivity} = 1 - \left( \frac{\text{var}_{\text{obs}} - \text{var}_{\text{min}}}{\text{var}_{\text{max}} - \text{var}_{\text{min}}} \right)$$

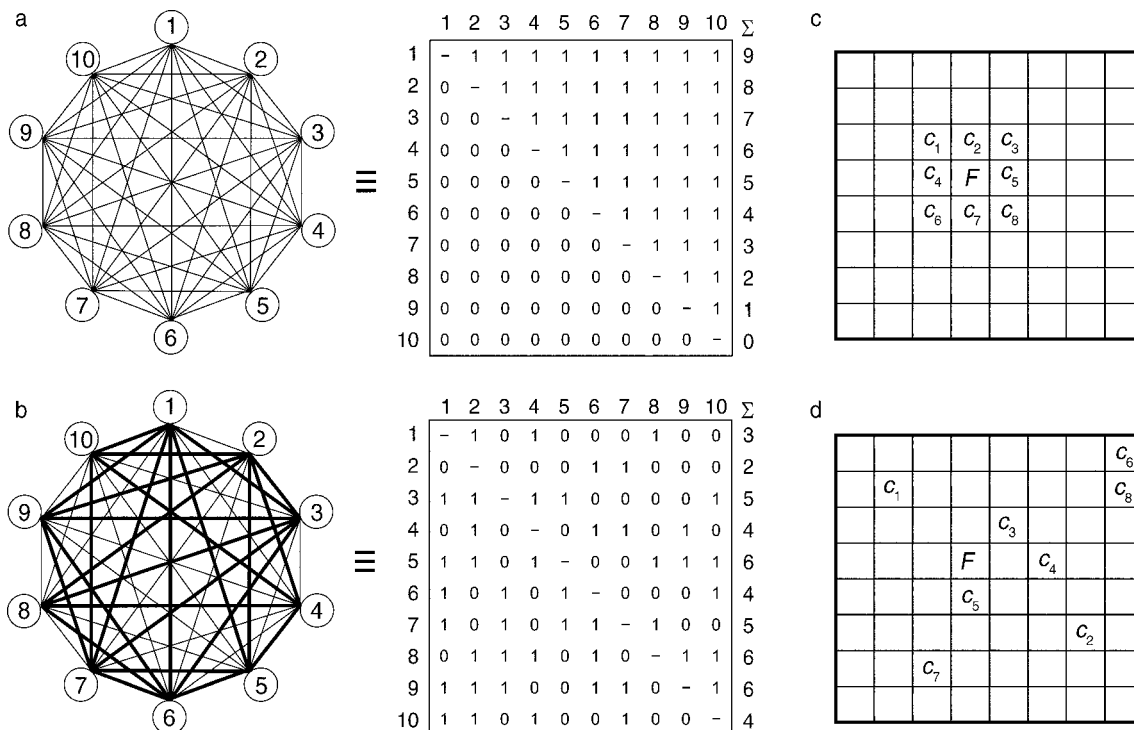


FIG. 1. (a, b) Examples of interaction webs and equivalent competitive-outcomes matrices for model communities with 10 species (numbered 1–10). In the interaction webs, thin lines connect species pairs for which the lower-numbered species outcompetes the higher-numbered species, while thick lines (panel b only) connect species pairs for which the higher-numbered species outcompetes the lower-numbered species. In the competitive-outcomes matrices, a 1 at position  $[i, j]$  means that species  $i$  outcompetes species  $j$ ; a 0 means the converse. The elements of the leading diagonal are defined as blanks (designated with –). The column to the right of the matrices ( $\Sigma$ ) contains the row sums (i.e., the numbers of species that the species designated by each row outcompetes). More intransitive competitive-outcomes matrices have a lower variance in these row sums and, hence, a higher relative intransitivity. (a) A perfectly transitive/hierarchical competitive community (relative intransitivity = 0). (b) A highly intransitive/networked competitive community (relative intransitivity = 0.825). (c, d) Examples of “competition events” taking place in a simplified  $8 \times 8$  cell lattice, in which every cell is occupied by an individual competitor. (c) When competition is local, the randomly chosen focal individual ( $F$ ), is replaced only if at least one of the eight potential competitors ( $c_1$ – $c_8$ ) in its  $3 \times 3$  cell neighborhood is a superior competitor. (d) When competition is global, the eight potential competitors are chosen from random locations in the lattice. Keeping the number of potential competitors constant (i.e., eight per competition event) prevents confounding the spatial arrangement of competitors with the number of competitors. Note that our actual simulations used a  $100 \times 100$  cell lattice with periodic boundaries.

where  $\text{var}_{\text{obs}}$  is the variance of the row sums of the observed competitive-outcomes matrix (i.e., the variance in the number of species that each species outcompetes;  $\Sigma$  columns in Fig. 1a, b), and  $\text{var}_{\text{max}}$  and  $\text{var}_{\text{min}}$  are, respectively, the maximum and minimum possible variances for the row sums of a competitive-outcomes matrix with the same number of species as the observed competitive-outcomes matrix. The index has high values (maximum = 1) when each of the  $s$  competing species is dominant to approximately the same number of other species (i.e., intransitive or networked competition). Conversely, the index has low values (minimum = 0) when the numbers of species that each species outcompetes are distributed unequally (i.e., transitive or hierarchical competition). Relative intransitivity is highly negatively correlated with Petraitis’  $t$  (Petraitis 1979), a more traditional index of intransitivity that takes a prohibitively long time to calculate when  $s > 9$  (see Laird and Schamp 2006).

*Modeling competition*

*Local competition.*—Our model simulated competition between  $s$  species in a  $100 \times 100$  cell lattice with periodic boundaries, where  $s = 3$ –25. We ran 100 iterations of the model per value of  $s$ . Each iteration’s competitive-outcomes matrix was determined randomly, in such a way as to achieve a suite of competitive-outcomes matrices with an approximately uniform distribution of relative intransitivity values between 0 and 1.

Initially, individuals from the  $s$  species were distributed randomly and independently throughout the lattice. During each competition event, a focal individual (cell) was chosen at random, and was subjected to potential competitive replacement by a competitively superior individual, if such an individual was located in the focal individual’s  $3 \times 3$  cell neighborhood (Fig. 1c). If the neighborhood contained individuals of more than one competitively superior species, the probability of

TABLE 1. Results of ANOVA on the number of generations until the first extinction (log-transformed; see Fig. 2).

Source	df	SS	F	P
Intransitivity	4	165.26	1664.88	<0.0001
Localness	1	4.41	177.55	<0.0001
Richness	20	15.61	31.45	<0.0001
Intrans. $\times$ localness	4	3.94	39.74	<0.0001
Intrans. $\times$ richness	80	6.32	3.18	<0.0001
Localness $\times$ richness	20	0.53	1.08	0.37
Intrans. $\times$ localness $\times$ richness	80	2.01	1.01	0.45
Error	3946	97.92		

*Notes:* The independent categorical variables were competitive intransitivity (relative intransitivity split into five equally sized categories), the localness of competition, and initial species richness. Data for model runs in which there were initially three or four species were excluded because not all of the relative intransitivity categories are possible for  $s < 5$  (where  $s$  is the number of competing species; see Fig. 2). Data for model runs in which the number of generations until the first extinction was unknown (i.e.,  $>500$ ) were also excluded (see *Methods: Analyses*). All two- and three-way interactions were also included in the model. The ANOVA on untransformed data (not shown) yielded qualitatively similar results (i.e., the same main factors and interactions were significant).

replacement by each competitively superior species was proportional to its relative incidence in the neighborhood. Ten-thousand competition events constituted one model “generation,” so that on average, each of the  $100^2$  cells was subjected to one competition event per generation. Each iteration continued until the model community became a monoculture, or to 500 generations, whichever came sooner. We considered two measures of species coexistence, the number of generations until the first extinction (short-term coexistence) and the final species richness at the end of one iteration (long-term coexistence).

*Global competition.*—The only difference between the local and global competition models was the absence of spatially explicit interactions in the latter. During each competition event, rather than having the focal individual compete with the eight other individuals in its  $3 \times 3$  cell neighborhood, it instead competed with eight individuals chosen at random from the entire lattice (Fig. 1d). The probability that the focal individual was replaced by any given competitively superior species was, on average, proportional to the global relative incidence of that competitively superior species, similar to mean field approximations. Yet, by only allowing eight competitors at a time, we were able to compare local and global competition directly, without confounding the spatial aspects of competition with the number of competitors.

*Example model runs.*—To aid in the visualization of our models, we recorded movies depicting six-species competition. We used two levels of the “localness” of competition (local and global) and two levels of intransitivity (relative intransitivity of 1 and 0), for a total of four community types (local-hierarchical, local-intransitive, global-hierarchical, and global-intransitive).

For a single iteration of each community type, the movie recorded changes in the composition and spatial arrangement of each  $100 \times 100$  cell lattice for the first 20 generations after initial seeding or until monoculture, whichever came first. These four movies are available in Appendix A (Fig. A1), along with four time-series tracking species richness, evenness ( $E_{\text{var}}$ ; Smith and Wilson 1996), and aggregation patterns across generations (Appendix A: Fig. A2). The aggregation index we used was  $AI_i$ , which we modified from He et al. (2000) to work with the periodic boundaries of our lattices.  $AI_i$  is the number of edges in a lattice shared by pairs of individuals of species  $i$ , relative to the maximum possible value of this quantity (He et al. 2000). Thus,  $AI_i$  has a maximum of 1 (maximally aggregated) and a minimum of 0 (completely disaggregated).

#### *Examining the role of spatial aggregation*

Our simulations showed that local competition enhanced intransitivity-mediated coexistence in the short term, yet hindered it in the long term (see *Results*). The example movies and time series of six-species competition suggested a possible mechanism for this unexpected result (Appendix A: Figs. A1 and A2). Specifically, while local intransitive competition might slow the rate of species extinctions in the short-term by allowing for the formation and persistence of species aggregations, when species eventually become disaggregated, local competition might actually speed their long-term extinction rate as they become surrounded by superior competitors. To test this idea, we performed a post hoc analysis examining the development of spatial patterns in relation to extinction events under both local and global competition. We ran 50 iterations of our model exploring both local and global competition for communities with an initial species richness of  $s = 19$  (chosen arbitrarily). We tracked the aggregation of all species for 500 generations. For each species that became completely disaggregated (i.e., when every individual was surrounded by other species), we recorded the number of generations until its first complete disaggregation. For each species that subsequently went extinct, we also recorded the number of generations between its first complete disaggregation and its extinction.

#### *Analyses*

Our first measure of species coexistence was the number of generations until the first extinction event. Before analysis, it was necessary to exclude the small number of extinction-free iterations (137 out of 4600 iterations), because in these cases the number of generations until the first extinction was unknown (but  $>500$ ). Fisher’s exact tests revealed that there were no effects ( $P > 0.05$ ) of the localness of competition on the proportion of extinction-free iterations for all but one of the 23 species richness levels. Following this data-culling

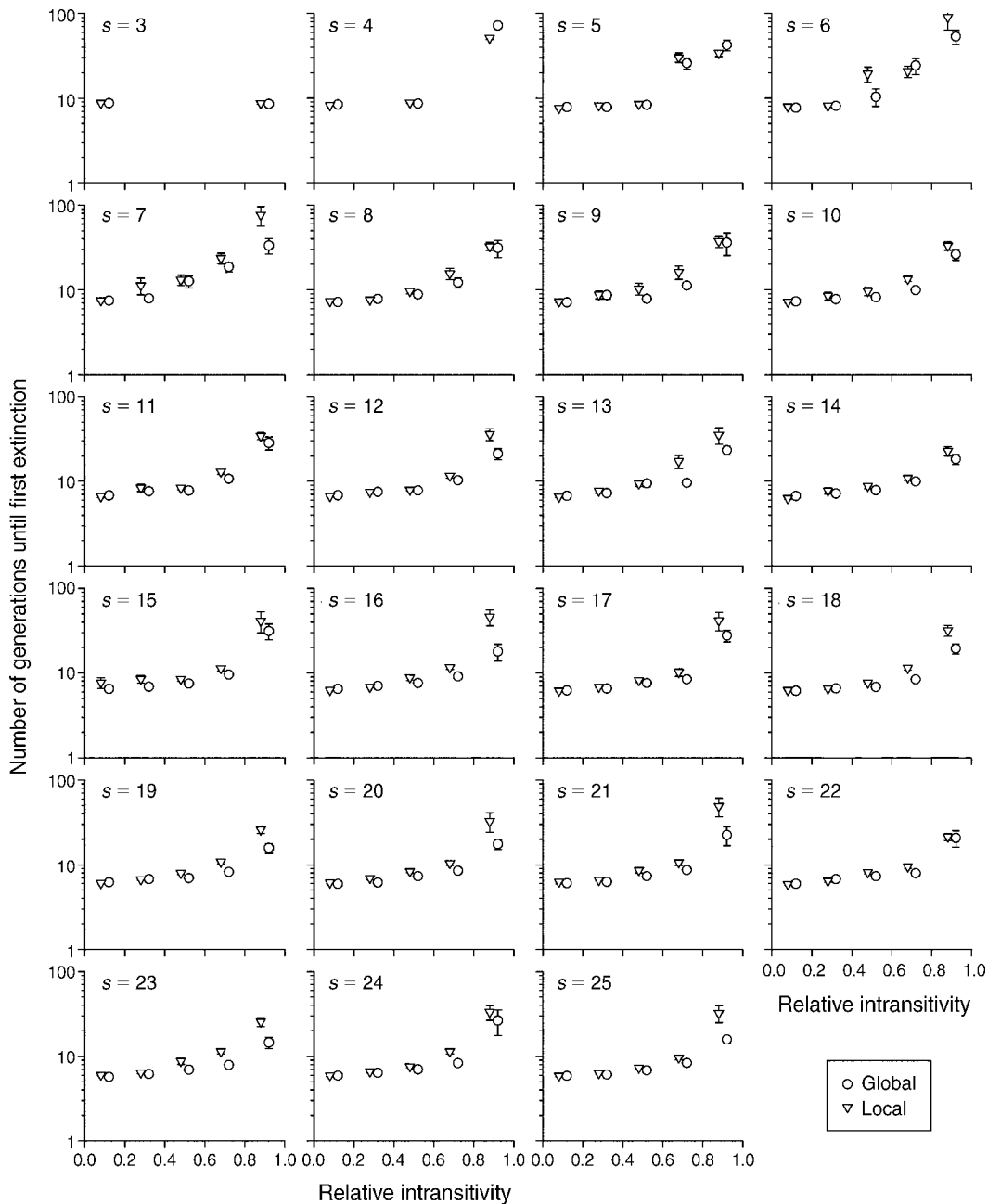


FIG. 2. Number of generations until the first extinction ( $y$ -axis; note the log scale) as a function of initial species richness ( $s$ , different for each panel), competitive intransitivity (initial relative intransitivity, split into five equally sized categories,  $x$ -axis), and localness of competition (circles represent global competition; triangles represent local competition). Symbols and error bars represent means and standard errors, respectively. Communities that did not experience an extinction event over the 500 generations were excluded (see *Methods: Analyses* for details). The statistical analysis accompanying these data is found in Table 1. See Fig. B1 in Appendix B for a similar figure showing the raw (non-categorized) data.

procedure, we analyzed generation until first extinction using a three-way ANOVA with the following independent variables: initial relative intransitivity (five levels between 0 and 1, with each level comprising a 0.2 interval), localness of competition (two levels: local and global), and initial species richness (21 levels, 5–25 species; below  $s = 5$ , some of our levels of relative

intransitivity are impossible; therefore, data for  $s = 3$  or  $s = 4$  were omitted from the analysis). All two- and three-way interactions were also included. The ANOVA was performed on log-transformed data to homogenize variances; however, this log-transformation did not affect the qualitative conclusions of the ANOVA model (not shown).

TABLE 2. Results of ANOVA on final species richness (see Fig. 3).

Source	df	SS	F	P
Intransitivity	4	25 759.24	2243.46	<0.0001
Localness	1	526.63	183.46	<0.0001
Richness	20	7137.40	124.32	<0.0001
Intrans. $\times$ localness	4	723.56	63.02	<0.0001
Intrans. $\times$ richness	80	3590.96	15.64	<0.0001
Localness $\times$ richness	20	270.29	4.71	<0.0001
Intrans. $\times$ localness $\times$ richness	80	546.68	2.38	<0.0001
Error	3990	11 453.21		

*Notes:* The independent categorical variables were competitive intransitivity (relative intransitivity split into five equally sized categories), the localness of competition, and initial species richness. Data for model runs in which there were initially three or four species were excluded because not all of the relative intransitivity categories are possible for  $s < 5$  (where  $s$  is the number of competing species; see Fig. 3). All two- and three-way interactions were also included in the model.

We used an analogous three-way ANOVA to analyze our second measure of species coexistence, the final species richness at the end of one iteration. In this case, however, log-transformation was unnecessary. Also, since final species richness was always an exactly known quantity, it was not necessary to exclude any additional iterations, other than those for which  $s = 3$  or  $s = 4$ .

For our 19-species post hoc analysis, we used Wilcoxon rank sum tests to test for differences between locally and globally competing communities in both the number of generations until the first complete disaggregation, and the interval between a species' disaggregation and its extinction.

## RESULTS

### *Number of generations until first extinction*

Intransitive competition significantly delayed the time until first extinction (Table 1, Fig. 2; Appendix B: Fig. B1), from six to eight simulated generations in hierarchical competition to sometimes more than 30 or 40 generations in highly intransitive competition. Species richness had a highly significant effect on the time until first extinction (Table 1), such that initially species-rich communities generally lost their first species more quickly than initially species-poor communities (Fig. 2). The effect of initial species richness on the time until first extinction was conditional on competitive intransitivity (Table 1): when intransitivity was low, first extinctions occurred at approximately the same time across levels of initial species richness; however, when intransitivity was high, first extinctions typically occurred sooner in initially species-rich communities than in initially species-poor communities (Fig. 2). There was also a highly significant main effect of the localness of competition on time until first extinction (Table 1), with first extinctions occurring later with local competition than with global competition (Fig. 2). While the overall effect of intransitivity on time until extinction was

positive whether competition was local or global, there was a significant interaction between competitive intransitivity and the localness of competition (Table 1): competitive intransitivity slowed the time until first extinction more in local competition than in global competition (Fig. 2). Thus, in terms of generations until first extinction, the significant interaction between intransitivity and localness of competition conformed to our primary hypothesis.

### *Final species richness*

As with generations until first extinction, final species richness was strongly and positively dependent on intransitivity (Table 2, Fig. 3; Appendix B: Fig. B2). Initial species richness also had a strongly positive main effect on final species richness (Table 2). This is unsurprising: communities that started off with more species ended up with more species. Related to this was the significant interaction between intransitivity and initial species richness (Table 2), which also occurred due to the constraint imposed by initial richness on final richness. More interestingly, and unexpectedly, the localness of competition had a highly significant main effect on final species richness (Table 2), with globally competing communities having greater final species richness than locally competing communities (Fig. 3). This effect of the localness of competition on final species richness was contingent on both intransitivity and initial species richness (Table 2): low-intransitivity communities had similarly low final species richness regardless of the localness of competition, whereas highly intransitive, globally competing communities had greater final species richness than their locally competing counterparts, an interaction that became more pronounced with increasing initial species richness (Fig. 3). Thus, the significant interaction between intransitivity and localness was not as predicted by our primary hypothesis: global, not local competition enhanced intransitivity-mediated coexistence in terms of final species richness.

### *The role of spatial aggregation*

Species in locally competing, 19-species communities took significantly longer to reach complete disaggregation (Fig. 4a). In contrast, after species became completely disaggregated, the loss of those species was significantly slower in globally competing communities than in locally competing communities (Fig. 4b).

## DISCUSSION

Our results show that intransitivity and the localness of competition interact to determine coexistence, measured as the number of generations until the first extinction event, and final species richness after 500 generations (Figs. 2 and 3, respectively). Interestingly, this interaction differed for our two measures of species coexistence. In general, locally competing communities experienced coexistence longer before their first extinc-

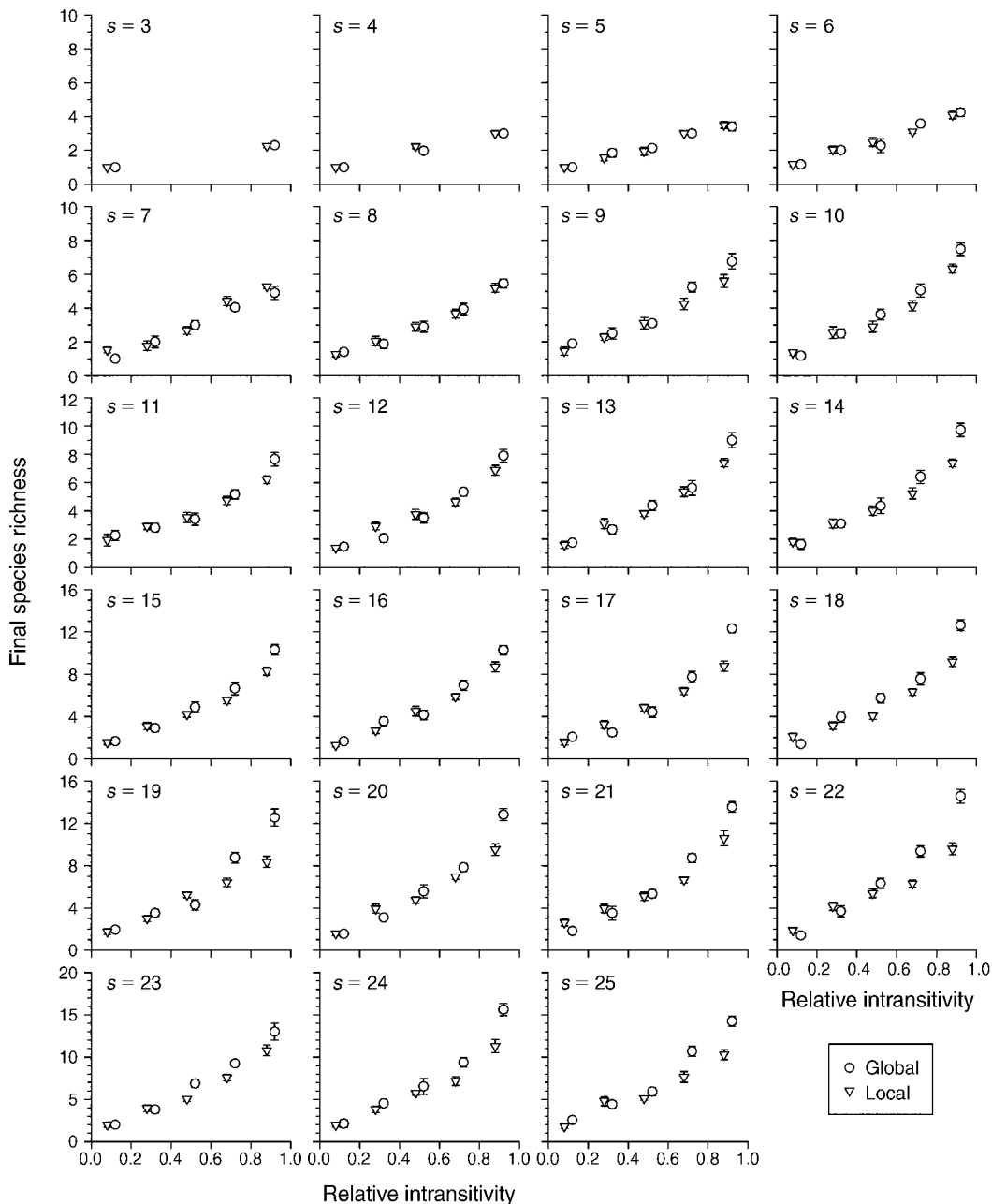


FIG. 3. Final species richness ( $y$ -axis) as function of initial species richness ( $s$ , different for each panel), competitive intransitivity (initial relative intransitivity, split into five equally sized categories,  $x$ -axis), and localness of competition (circles represent global competition; triangles represent local competition). Symbols and error bars represent means and standard errors, respectively. Note the differently scaled  $y$ -axes among rows of panels. The statistical analysis accompanying these data is found in Table 2. See Fig. B2 in Appendix B for a similar figure showing the raw (non-categorized) data.

tion event: an effect that was stronger at higher levels of intransitivity (Fig. 2). While this finding supports the theoretical prediction that local competition initially slows species loss, accentuating intransitivity-mediated coexistence, we also observed that locally competing intransitive communities had fewer species remaining after 500 generations (Fig. 3). Therefore, in our model, local competition enhanced intransitivity-mediated

species coexistence in the short term, but reduced it in the long term, compared to global competition. This result was unexpected and challenges the generally accepted positive effect that local interactions are thought to have on intransitivity-mediated coexistence (Durrett and Levin 1997, 1998, Kerr et al. 2002) and on coexistence in general. A negative impact of local interactions on coexistence, however, is not unprece-

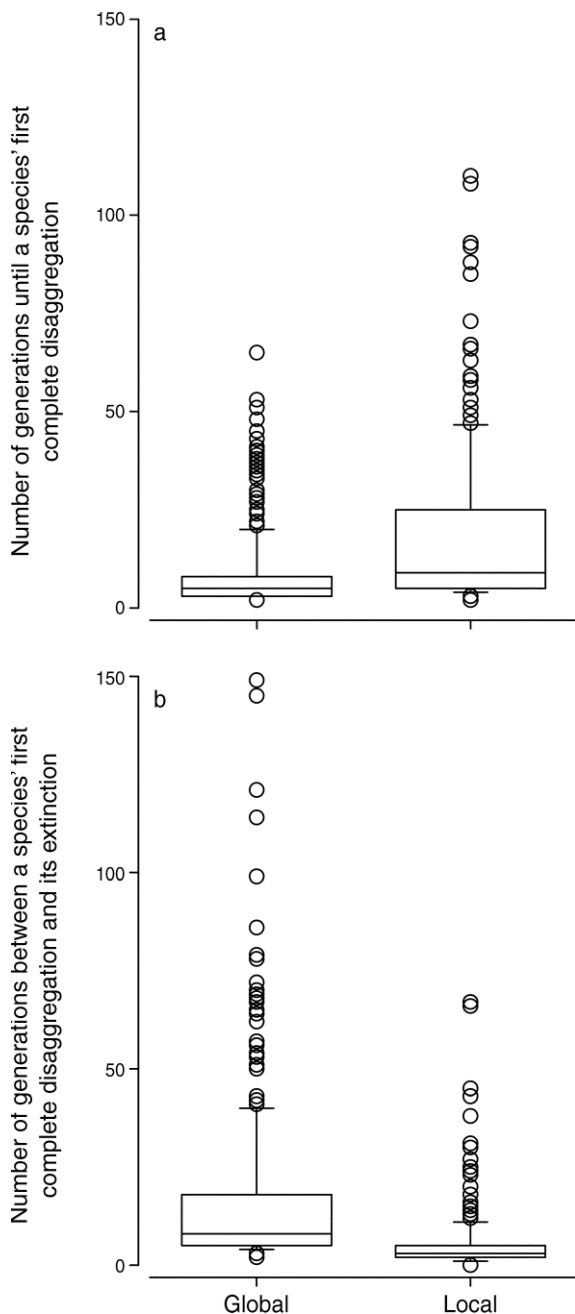


FIG. 4. Box plots for (a) the number of generations until the first complete disaggregation for globally and locally competing species ( $s = 19$  species), and (b) the number of generations between the first disaggregation and the extinction of the disaggregated species. The whiskers represent the 10th and 90th percentiles, the bottom and top edges of the boxes represent the 25th and 75th percentiles, the lines inside the boxes are the medians, and the points represent data that fell outside the 10th or 90th percentiles. In both cases, the  $y$ -axes were truncated at 150 generations, since this interval contained nearly all the data (in panel a, there were 0 and 7 data points beyond generation 150, for global and local competition, respectively; in panel b, there were 3 and 0 data points beyond generation 150 for global and local competition, respectively). The number of generations until first complete disaggregation was significantly greater for

dent. For example, Hauert and Doebeli (2004) observed that local interactions can negatively impact the coexistence of cooperative and uncooperative strategies in an evolutionary “snowdrift” model. Additionally, Neuhauser and Pacala (1999) found that in a spatial model of Lotka-Volterra competition, local competition reduced the parameter space under which coexistence occurred, suggesting a potential negative impact of local interactions.

The contrasting effects of local and global competition on short- and long-term intransitivity-mediated coexistence result from differences in the emergence and the consequences of spatiotemporal patterns of species aggregation and disaggregation. Local intransitive competition results in increased levels of aggregation because each species can only grow in abundance through local spread (e.g., Fig. 5a). These aggregations tend to develop less in global competition because of continual mixing (e.g., Fig. 5b). When aggregated, most individuals of a given species are surrounded by conspecifics, buffering them from interspecific competition with competitively superior species (e.g., Pacala 1986, Rees et al. 1996, Murrell et al. 2001, Monzeglio and Stoll 2005). Therefore, local intransitive competition promotes increased short-term coexistence by slowing the process of disaggregation (Fig. 4a). However, during local competition, once individuals of a species are completely disaggregated and surrounded by superior competitors (i.e., once the advantages of local competition break down), that species can no longer increase in abundance (e.g., Fig. 5c). Yet in global competition, there is a chance that individuals of such a species could end up beside inferior competitors, allowing that species to maintain or increase its abundance. Accordingly, once a species becomes completely disaggregated, local competition leads to significantly faster extinction of that species compared to global competition (Fig. 4b). In other words, an “island” of local competitors has no way to escape a “sea” of competitive superiors, whereas global competitors have a small chance of being mixed beside individuals of a species they can outcompete. In this way, global rather than local competition contributes to increased long-term intransitivity-mediated coexistence by slowing the process of exclusion when a species becomes relatively disaggregated or rare. In this manner, dispersal, which is one mechanism for “global” interactions, may act as a potential refuge for rare,

← locally competing species than for globally competing species (Wilcoxon rank sum test;  $Z = -10.01$ ;  $P < 0.0001$ ;  $N_L = 353$ ,  $N_G = 332$ , where  $N_L$  and  $N_G$  are, respectively, the total number of initial disaggregation events across all iterations for local and global competition). The number of generations between complete disaggregation and the extinction of the disaggregated species was significantly smaller for locally competing species than for globally competing species (Wilcoxon rank sum test,  $Z = 13.63$ ,  $P < 0.0001$ ,  $N_L = 353$ ,  $N_G = 332$ ).



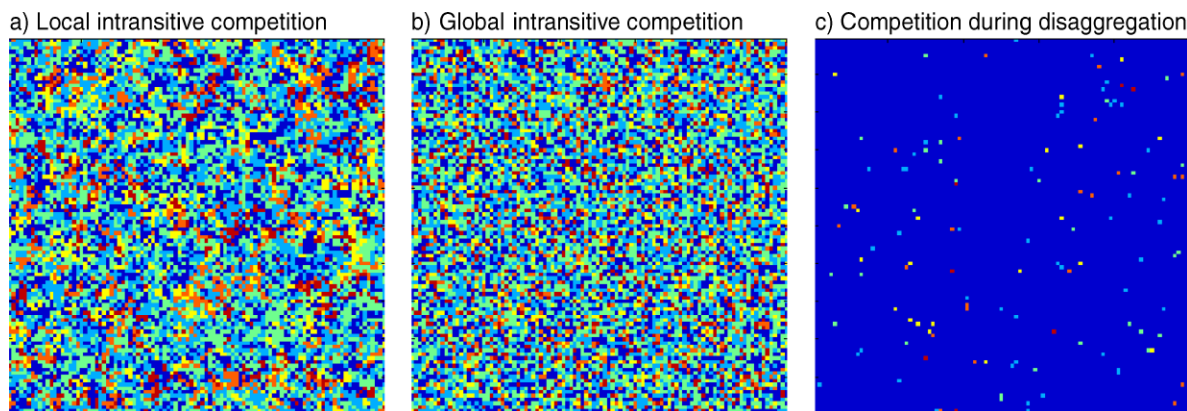


FIG. 5. Three “snapshots” of multispecies competition from our simulation model illustrating why local competition promotes intransitivity-mediated coexistence in the short term, but not in the long term. In these snapshots, like-colored cells represent individuals of a competing species. In (a), competition is “local” and only occurs between members of  $3 \times 3$  cell neighborhoods (see Fig. 1c). When competition is local, species aggregations form spontaneously, allowing weaker competitors to coexist with stronger competitors by occupying ephemeral, shifting refuges. These refuges cannot form when competition is global, e.g., in well-mixed environments (panel b; see Fig. 1d). Spatial refuges lead to a longer time until the first species goes extinct in locally vs. globally competing systems; therefore, local competition promotes short-term species coexistence. However, strong competitors eventually wear down spatial refuges, causing weaker competitors to become disaggregated (e.g., the effects of the “blue” species; panel c). When this happens, local competition hinders species coexistence, because once individuals become surrounded by superior competitors, their rapid competitive exclusion is inevitable. Conversely, in global competition, competitive subordinates can “escape” competition if environmental mixing moves them to a more favorable location.

competitively inferior species. This is similar to the effect of dispersal in a competition/colonization tradeoff (e.g., Tilman 1994); however, our results show that such a trade-off is not necessary for global interactions to promote long-term intransitivity-mediated coexistence.

An alternative explanation for the reversal in the effect of local vs. global intransitive competition on short- and long-term coexistence is that while extinction initially occurs relatively slowly in locally competing communities, it may lead to progressively depauperate communities with species compositions that are more prone to extinction than those that arise in globally competing communities. In Appendix C, we show that this alternative explanation can be rejected.

The effect of local and global competition on intransitivity-mediated coexistence was relatively small, especially for more hierarchical model communities (Figs. 2 and 3). In combination with the contrasting effects of local and global competition on short- and long-term coexistence, our findings suggest that intransitivity has the potential to play an important role in maintaining diversity in globally interacting systems, in addition to the locally interacting systems to which the importance of intransitivity is more frequently ascribed. Huisman and Weissing (1999, 2001a, b) have modeled one kind of intransitivity-mediated coexistence in globally competing phytoplankton communities using a model of competition for multiple resources. Their model demonstrates that intransitivity based on trade-offs in competitive ability for three to four nutrients can result in the coexistence of many species. While there is evidence for such trade-offs in competitive ability for phosphorus and silica between freshwater diatom

species (Tilman 1981, van Donk and Kilham 1990) and for nitrogen and silica between marine algae (Sommer 1986), another study found no trade-off in competitive ability for phosphorus and light (Passarge et al. 2006), and to our knowledge, no study has yet tested for trade-offs in competitive ability for more than two resources within a single group of species. Estimating intransitivity in extremely diverse phytoplankton communities remains an important challenge.

A great deal of research has focused on the impact of local interactions on species coexistence (e.g., Rees et al. 1996, Durrett and Levin 1997, 1998, Kerr et al. 2002, Miyazaki et al. 2006). However, even systems that are traditionally viewed as well mixed, such as phytoplankton communities, experience imperfect mixing through time (Károlyi et al. 2000, 2005). Such imperfect mixing is likely characteristic of many communities, and in most biological systems spatial interactions will not be strictly local or global, but rather fall somewhere in between these two extremes (e.g., Zhang et al. 2006). Indeed, just as traditionally “global” communities may exhibit aspects of local competition, traditionally “local” communities may exhibit aspects of global competition. Even sessile marine benthic communities and plant communities, which compete locally within generations, can be thought of as competing circumglobally across generations (i.e., different scales of dispersal and competition [sensu Ellner 2001, Dunstan and Johnson 2005]). For example, while dispersal among many plants is predominantly local, seed shadow distributions vary widely among species and are generally characterized by long tails (Willson 1993, Nathan and Muller-Landau 2000). In particular, annual plant communities, consist-

ing of short-lived species with long seed-bank dormancy and strong dispersal, may be characterized by both local and global interactions.

### Conclusions

Our model demonstrates that there is previously unappreciated diversity in the interactive effects of intransitivity and the localness of competition on species coexistence. Specifically, local competition can enhance intransitivity-mediated coexistence in the short-term, but reduce it in the long-term. The importance of this in ecological communities will naturally depend on the time scales of other mechanisms of coexistence. For example, in communities with periodic or episodic disturbance, local competitive interactions may promote intransitivity-mediated coexistence if the average inter-disturbance interval is sufficiently short.

The finding that there is a reversal in the effects of the localness of intransitive competition is a significant departure from previous work that focused on the benefits, rather than the costs, of local competition on coexistence, and it contributes to our understanding of coexistence in a wide range of biological communities that vary in intransitivity and the spatial pattern and scale of interactions. From a theoretical perspective, future work should relax some simplifying assumptions of our model, in particular allowing for the incorporation of empirically supported competition models and more subtle variations in the mixing patterns of communities. From an empirical perspective, studies that increase understanding of the prevalence and strength of intransitivity in natural communities, as well as quantify spatial aspects of competition, would be most valuable.

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#### APPENDIX A

Movies of the lattice model depicting six-species competition, varying the localness of competition (“local” vs. “global”) and the level of intransitivity (“hierarchical” vs. “intransitive”) (*Ecological Archives* E089-013-A1).

#### APPENDIX B

Figures showing the raw data for the number of generations until the first extinction and final species richness (*Ecological Archives* E089-013-A2).

#### APPENDIX C

Discussion of an alternative explanation for the reversal in the effect of local vs. global intransitive competition on short- and long-term coexistence (*Ecological Archives* E089-013-A3).