

Competitive Intransitivity Promotes Species Coexistence

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ABSTRACT: Using a spatially explicit cellular automaton model with local competition, we investigate the potential for varied levels of competitive intransitivity (i.e., nonhierarchical competition) to promote species coexistence. As predicted, on average, increased levels of intransitivity result in more sustained coexistence within simulated communities, although the outcome of competition also becomes increasingly unpredictable. Interestingly, even a moderate degree of intransitivity within a community can promote coexistence, in terms of both the length of time until the first competitive exclusion and the number of species remaining in the community after 500 simulated generations. These results suggest that modest levels of intransitivity in nature, such as those that are thought to be characteristic of plant communities, can contribute to coexistence and, therefore, community-scale biodiversity. We explore a potential connection between competitive intransitivity and neutral theory, whereby competitive intransitivity may represent an important mechanism for "ecological equivalence."

Keywords: biodiversity, cellular automaton, competition, intransitivity, species coexistence, transitivity.

Explaining species coexistence is one of the most important problems in community ecology. One of the greatest challenges lies in reconciling the undeniable fact of coexistence with the competitive-exclusion principle. Attempts to reconcile this "paradox" have focused on factors that mitigate competitive exclusion and therefore promote coexistence (e.g., disturbance, predation, niche differentiation, and habitat heterogeneity; reviewed by Tokeshi

[1999]). Here, using a spatially explicit cellular automaton model with local competition, we show that intensely competing species can coexist even in the absence of these "mechanisms of mitigation," provided that some inter-specific competition is intransitive, rather than hierarchical.

The concept of competitive intransitivity (also called nontransitivity, competitive networks, competitive loops, or competitive cycles; Gilpin 1975; Jackson and Buss 1975; May and Leonard 1975; Petraitis 1979) can be explained most simply using a hypothetical three-species system (species A, B, and C). Assuming that each of these species competes with the other two in a deterministic fashion, there are two possible competitive scenarios: perfectly intransitive competition and perfectly hierarchical competition. Perfectly intransitive competition among these three species occurs when, for example, species A outcompetes species B, B outcompetes C, and C outcompetes A (sometimes written as $A > B > C > A$). Alternatively, hierarchical competition (also referred to as perfectly transitive or perfectly nested competition) occurs when the three species can be listed unambiguously in order of their competitive abilities: for example, species A outcompetes species B and C, and species B outcompetes species C ($A > B > C$). For this simplified three-species system, these two extreme cases are the only possible competitive scenarios. When more species are added to the system, however, intermediate scenarios become possible whereby communities with equal species richness can have different levels of intransitivity, ranging from perfect intransitivity to a perfect hierarchy. Hereafter, the term "intransitivity" refers to the degree to which a system or focal group of species tends toward perfect intransitivity, rather than the condition of perfect intransitivity itself (as described above; *sensu* Petraitis 1979). Likewise, the term "transitivity" refers to the degree to which a system or group of species tends toward a perfect hierarchy.

Theory predicts several ways that intransitive competition can occur. First, under exploitation competition for multiple resources, intransitive competition can occur if each competitor competes best for, yet is limited by, a different resource (Huisman and Weissing 1999, 2001a, 2001b; Huisman et al. 2001). Second, under simultaneous

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interference and exploitation competition, intransitive competition can occur if species' ranks of exploitation competitive ability differ from their ranks of interference competitive ability (Gilpin 1975; Szabó and Czárán 2001*b*; Czárán et al. 2002). Finally, intransitivity can result from pure interference competition under particular arrangements of toxicity, susceptibility, and resistance (Czárán et al. 2002).

The mechanism by which intransitivity promotes coexistence is a simple one. In an intransitive three-species system, the competitors can coexist indefinitely, in spite of the fact that they all differ in competitive ability (e.g., Gilpin 1975; May and Leonard 1975; Durrett and Levin 1998; Huisman and Weissing 1999, 2001*b*; Kerr et al. 2002). Coexistence occurs because, although there are winners in pairwise competitive interactions, no single competing species is superior to any other at the level of the community. This competitive "equivalence" occurs because each species outcompetes and is outcompeted by an equal number of competitors. The strength of this theory is that it allows for coexistence while competition remains an important force in local dynamics.

Despite the intuitive simplicity that intransitivity offers as an explanation for species coexistence, the majority of research on the subject has been theoretical (Gilpin 1975; May and Leonard 1975; Karlson and Jackson 1981; Huisman and Weissing 1999, 2001*a*, 2001*b*; Huisman et al. 2001). This is surprising, given that many researchers have found evidence of intransitivity (Buss and Jackson 1979; Buss 1980; Taylor and Aarssen 1990; Shipley 1993 and references therein; Sinervo and Lively 1996) and competitive rank reversals (Chornesky 1989; Bowers 1993; Clay et al. 1993; Rejmánek and Lepš 1996; Cerdá et al. 1997; Rebele 2000; Suding and Goldberg 2001) in a number of natural systems and for a wide array of taxa. The focus on theory reflects several practical barriers to the empirical study of the relationship between competitive intransitivity and coexistence, such as measuring competitive ability appropriately (Freckleton and Watkinson 1999; Aarssen and Keogh 2002) and dealing with the prohibitively large sample sizes required to determine all pairwise competitive outcomes in species-rich assemblages. Hence, most studies of competitive ability have focused on a small number of species (e.g., Tilman 1977: $s = 2$; Mitchley and Grubb 1986: $s = 6$; Wilson and Keddy 1986: $s = 7$; Goldberg and Landa 1991: $s = 7$; Suding and Goldberg 2001: $s = 3$; Karev 2003: $s = 3$) or on subsets of the pairwise combinations (e.g., Passarge et al. 2006). Furthermore, promising evidence that genotype-level intransitivity occurs within and among some plant species (Taylor and Aarssen 1990) has received little attention and has rarely been explored beyond the theoretical (Aarssen 1989, 2005; Szabó and Czárán 2001*a*, 2001*b*; Czárán et al. 2002; but see Kerr

et al. 2002). Therefore, the central questions of the degree of intransitivity that can be found in natural communities and the consequences of this to coexistence have yet to be conclusively answered, although the general consensus is that, at least in plant communities, competition is seldom, if ever, perfectly transitive (Keddy and Shipley 1989; Shipley 1993).

The potential importance of intransitivity in promoting species coexistence warrants both renewed efforts to overcome these practical barriers and further detailed theoretical investigations. Here we use a cellular automaton model to explore the theoretical potential for varied levels of competitive intransitivity to promote persistent species coexistence. This type of model has been used to show how intransitivity can affect coexistence under conditions of perfect intransitivity for three species/strains (Durrett and Levin 1998; Kerr et al. 2002), but there is very little information about the potential for intermediate levels of intransitivity to prevent competitive exclusion at more realistic levels of species richness (but see Karlson and Jackson 1981 for a simplified example of multispecies competition). We show that communities characterized by greater intransitivity are more resistant to species extinctions, and therefore are more likely to experience persistent species coexistence, than more transitive (i.e., hierarchical) communities.

Methods

Competitive-Outcomes Matrices

Competitive-outcomes matrices indicate the direction of pairwise competitive dominance among all s competing species in a community. Therefore, matrices are s rows \times s columns in size. A competitive-outcomes matrix is populated with 1s and 0s. A 1 at position [row = r , column = c] means that species r outcompetes species c (Petraitis 1979). If r outcompetes c , it follows that c is outcompeted by r , so position [c , r] is filled with a 0. (Here we define all elements of the leading diagonal—where $r = c$ —as blanks.) Thus, competitive-outcomes matrices are in a sense "antisymmetrical" about the leading diagonal. Figure 1 shows five interaction webs of competitive outcomes with their corresponding competitive-outcomes matrices.

As they are described here, these competitive-outcomes matrices describe a very simplified system of competition, as is common to cellular automaton models (Durrett and Levin 1994). Notably, they assume, first, that each species has the potential to compete with every other species (no niche separation), second, that no two species are competitively equivalent, at least not when examined as an isolated pair, and third, that the dominance-subordination

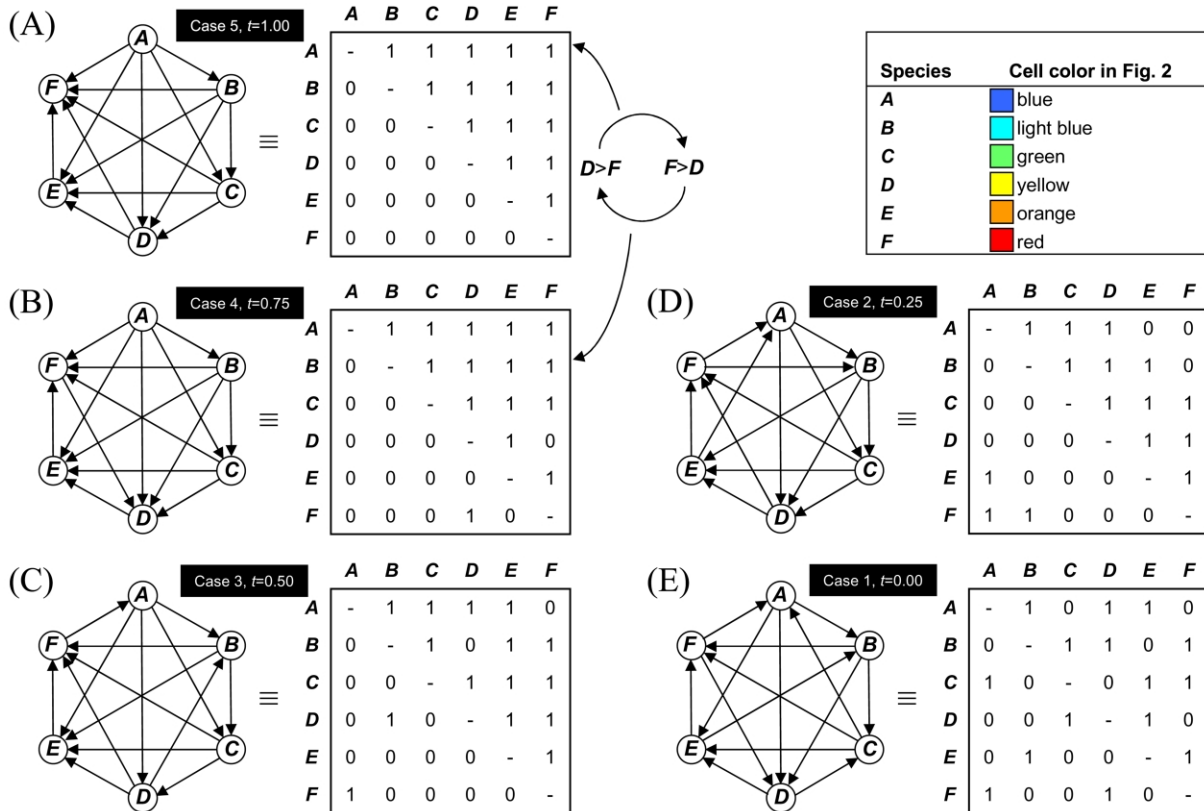


Figure 1: Interaction webs and equivalent competitive-outcomes matrices for $s = 6$ species (A, B, C, D, E, and F), with five different levels of competitive intransitivity. For each pairwise interaction in the interaction webs, arrows point from the competitive dominant to the competitive subordinate (e.g., if $A \rightarrow B$, then A is competitively dominant over B). In the competitive-outcomes matrices, a 1 indicates that the row species outcompetes the column species, while a 0 indicates the converse. For this reason, competitive-outcomes matrices are always “antisymmetrical” about the leading diagonal. See text for details. A, Case 5, a completely transitive (“hierarchical”) competitive scenario ($t = 1.0$). B, Case 4: a single competitive reversal ($D \rightarrow F$ becomes $F \rightarrow D$) produces a slightly more intransitive competitive scenario than in A ($t = 0.75$). C, Case 3 ($t = 0.5$; Petraitis 1979). D, Case 2 ($t = 0.25$; Petraitis 1979). E, Case 1 ($t = 0.0$, a perfectly intransitive competitive scenario; Petraitis 1979). The inset indicates the colors of lattice cells when occupied by species A–F in figure 2.

relations within pairs of species are strictly unidirectional and deterministic. Certainly, these assumptions do not embody the complexity of actual competitive outcomes in communities. They are, however, useful for testing the hypothesis that competitive intransitivity alone can promote species coexistence.

Indices of Competitive Intransitivity

Initially, we used Petraitis’s (1979) index of intransitivity, $t = 1 - s_p/M$, where s_p (not to be confused with s from above) is the minimum number of competitive reversals to change a given intransitive network into a perfect hierarchy and M is the maximum possible value of s_p for a given number of competitors. For a visual representation of a “competitive reversal,” contrast the relationships between species D and F in figure 1A and 1B. Petraitis’s

index has a maximum value of $t = 1$ when the competitors form a perfect hierarchy (e.g., fig. 1A) and a minimum value of $t = 0$ when competition between competitors is maximally intransitive (i.e., as far as possible from being a perfect hierarchy; fig. 1E).

While Petraitis’s t was our preferred index of intransitivity because of its explicit link with competitive reversals, in practice it is often too computationally expensive to be feasible, especially for the higher species richness values. This is because the number of possible competitive hierarchies that must be checked against the “observed” competitive-outcomes matrix increases with the factorial of species richness. Therefore, we sought an alternative index of competitive intransitivity that was both highly correlated with Petraitis’s t and much less computationally expensive. We noted that the distribution of the number of species outcompeted by each competitor in a com-

munity (i.e., the row sums in a competitive-outcomes matrix) is related to the level of intransitivity. For example, in a five-species community, if each species outcompetes two other species and is itself outcompeted by two other species, the distribution of “wins” is [2, 2, 2, 2, 2], and the community is perfectly intransitive. Likewise, in a perfect five-species hierarchy, the distribution of wins is [4, 3, 2, 1, 0] or some permutation thereof. Of all the possible distributions of wins, maximally intransitive competitive-outcomes matrices typically have the lowest possible variance, and maximally transitive competitive-outcomes matrices (i.e., perfect hierarchies) have the greatest possible variance. With this in mind, we developed a proxy index, which we refer to as “relative variance,” that scales the observed variance in the distribution of wins (var_{obs}) with the minimum and maximum possible values (var_{min} and var_{max} , respectively): $\text{relative variance} = (\text{var}_{\text{obs}} - \text{var}_{\text{min}}) / (\text{var}_{\text{max}} - \text{var}_{\text{min}})$. As with Petraitis’s t , the minimum value of relative variance is 0, occurring when $\text{var}_{\text{obs}} = \text{var}_{\text{min}}$ (a maximally intransitive community), and the maximum value of relative variance is 1, when $\text{var}_{\text{obs}} = \text{var}_{\text{max}}$ (a maximally transitive or perfectly hierarchical community). To test the correspondence between Petraitis’s t and our more convenient proxy index, relative variance, we randomly generated 100 competitive-outcomes matrices—and the associated t and relative variance—for species richness $s = 3$ –9. For $s = 3$, there was a perfect correspondence between the two indices ($r = 1$). For $s = 4$ –9, there were strong positive correlations between relative variance and Petraitis’s t (all $r > 0.85$, all $P < .0001$, all $n = 100$). On the basis of this evidence, we concluded that relative variance was suitable as a proxy index of intransitivity.

Note that Petraitis (1979) referred to t as a “measure of intransitivity” even though increasing values of t actually correspond to decreasing competitive intransitivity. For the sake of continuity, we have decided to keep his original, albeit mildly confusing, wording. This means that, for example, if species coexistence is negatively correlated with t and/or relative variance, it is positively correlated with intransitivity.

Spatially Explicit Cellular Automaton Simulations

We simulated the outcomes of local competition among multiple species using a spatially explicit cellular automaton model (Durrett and Levin 1994). The data set is available in a zip archive in the online edition of the *American Naturalist*, in both an Excel file and tab-delimited ASCII files; the archive also includes the Matlab code used

in the simulation.¹ We examined model competitive communities that initially had between $s = 3$ and $s = 25$ species. The dominance-subordinance relationships for each of the $s!/(2(s-2)!)$ species pairs were determined randomly, meaning that each iteration of the model operated under its own randomly constructed competitive-outcomes matrix. Species were distributed in a 100×100 -cell lattice with wraparound boundaries (i.e., a torus). At the start of each iteration, s species were seeded into the lattice randomly and independently, with each species having an equal probability of occupying any given cell. Each time step of the model corresponded to a competition event. A focal cell in the lattice was randomly chosen, and the individual occupying it was replaced with an individual of a competitively superior species, if one was present in the focal cell’s 3×3 “neighborhood” (i.e., the “Moore neighborhood”; Durrett and Levin 1994). If more than one superior competitor was present in the neighborhood, the occupant of the focal cell was randomly replaced by one of the superior competitors, with the probability of replacement of each superior competitor proportional to its relative incidence in the neighborhood, similar to the “proportional case” of Molofsky et al. (1999). Ten thousand time steps constituted one “generation,” so that, on average, every cell in the lattice was subjected to a competition event (Kerr et al. 2002). The model was run until the lattice became a monoculture or to a maximum of 500 generations. For each level of species richness examined, we ran 50 iterations of the model, for a total of 1,150 model runs.

Data Collection and Analysis

For each model iteration, we collected the following data after the lattice was originally seeded and again after each successive generation: the number of species remaining and the intransitivity (relative variance index) of the competitive-outcomes matrix of the remaining species. We sought to measure the effect of intransitivity on species coexistence; however, the setup of our model (i.e., no speciation or immigration) meant that, given enough time, we expected even the most intransitive competitive scenarios to result in species extinctions and ultimately tend toward monocultures. Thus, we used the number of species remaining at the end of the run (500 generations) and the number of generations until the first extinction as measures of species coexistence. It is important to note that these two measures of coexistence are not independent (i.e., communities for which it takes a relatively long time for the first extinction will typically have more species

¹ Code that appears in the *American Naturalist* has not been peer-reviewed, nor does the journal provide support.

remaining after 500 generations). We then used Spearman partial-correlation analysis to measure correlations between species coexistence and both initial species richness and competitive intransitivity. Our primary prediction was that species coexistence would be positively correlated with competitive intransitivity (i.e., negatively correlated with relative variance), after the effects of initial species richness were accounted for.

Sample Model Runs for $s = 6$ Species

To visualize the effects of varying degrees of competitive intransitivity on species coexistence, we also ran one additional model iteration for five example competitive scenarios, each of which corresponded to one of five different levels of competitive intransitivity for $s = 6$ species. The competitive-outcomes diagrams for the five cases are shown in figure 1. Cases 1–3 are equivalent to Petraitis's (1979) cases 1–3 and have intransitivity index values of $t = 0.00$, 0.25 , and 0.50 , respectively. Case 5 is perfectly transitive ($t = 1.00$), and case 4 ($t = 0.75$) is the same as case 5, except for a single competitive reversal (fig. 1). We recorded the state of the lattice after the initial seeding, at 1, 4, 16, 64, and 256 generations, and at the end of the run (500 generations). We also recorded the following data over the entire time series: species richness, species evenness, and competitive intransitivity. In this case, we used Petraitis's t as the index of intransitivity, because for $s = 6$, computing t requires a feasible computational time.

Results

Sample Model Runs for $s = 6$ Species

Figure 2 shows the state of the lattice after 0, 1, 4, 16, 64, 256, and 500 generations for one iteration of the model at each of five different levels of intransitivity and an initial species richness of $s = 6$. The competitive relationships for each of these five cases are shown in figure 1. The changes in species richness, evenness, and intransitivity for these five model runs are shown in figure 3.

Because of the random seeding of the lattices, all runs started with well-mixed communities with evenness (E_{var} ; Smith and Wilson 1996) values close to the maximum value of 1 (figs. 2, 3; high values of E_{var} reflect communities in which all species are similarly abundant, while low values of E_{var} characterize communities in which some species dominate while others are rare). Model communities operating under the most transitive competitive-outcomes scenarios (cases 5 and 4) decreased in species richness to monoculture within 12 generations (i.e., approximately 120,000 competitive events). More competitively intransitive communities (cases 3 and 2) lost only one species

over the course of 500 generations, with the more intransitive of the two, case 2, lasting more generations at $s = 6$ species before this single extinction event occurred (92 vs. 36 generations). The perfectly intransitive community, case 1, lasted 58% as long as case 2 before the first extinction (53 vs. 92 generations), but soon after it also lost two additional species, at generations 58 and 60.

Intransitivity can be calculated only when there are at least three species present in a community. Communities in which at least three species persisted for at least 500 generations (cases 3, 2, and 1: fig. 3C, 3D, and 3E, respectively) were either equally intransitive or more intransitive (i.e., had lower values of t) at the end of the 500 generations than they were initially.

Full Simulation Results for $s = 3$ –25 Species

The number of species remaining after 500 generations was positively partially correlated with initial species richness (fig. 4A). This is not surprising, since final and initial richnesses are not independent variables; rather, initial richness constrains the possible final richness values below the 1 : 1 line. More interestingly, however, the number of species remaining after 500 generations was also positively partially correlated with competitive intransitivity (i.e., negatively partially correlated with initial relative variance; fig. 4B). In other words, more competitively intransitive communities tended to have more species remaining at the end of the simulations, compared to more competitively transitive communities.

The other measure of species coexistence—the number of generations until the first extinction event—was negatively partially correlated with initial species richness (fig. 5A, 5C). This trend was largely driven by several highly intransitive three- and five-species communities that did not experience any extinction over the course of the simulations (contrast fig. 5A with fig. 5C). As with the number of species remaining at the end of the simulations, the number of generations until the first extinction was also positively partially correlated with competitive intransitivity (i.e., negatively partially correlated with initial relative variance; fig. 5B, 5D); it typically took longer for more intransitive communities to lose their first species to extinction, compared to more competitively transitive communities. Interestingly, there was greater variation in species coexistence at higher levels of intransitivity for both measures of species coexistence (fig. 6).

Discussion

The results of our simulations for $s = 3$ –25 species confirm our prediction that higher levels of intransitivity have increased potential for promoting species coexistence, even

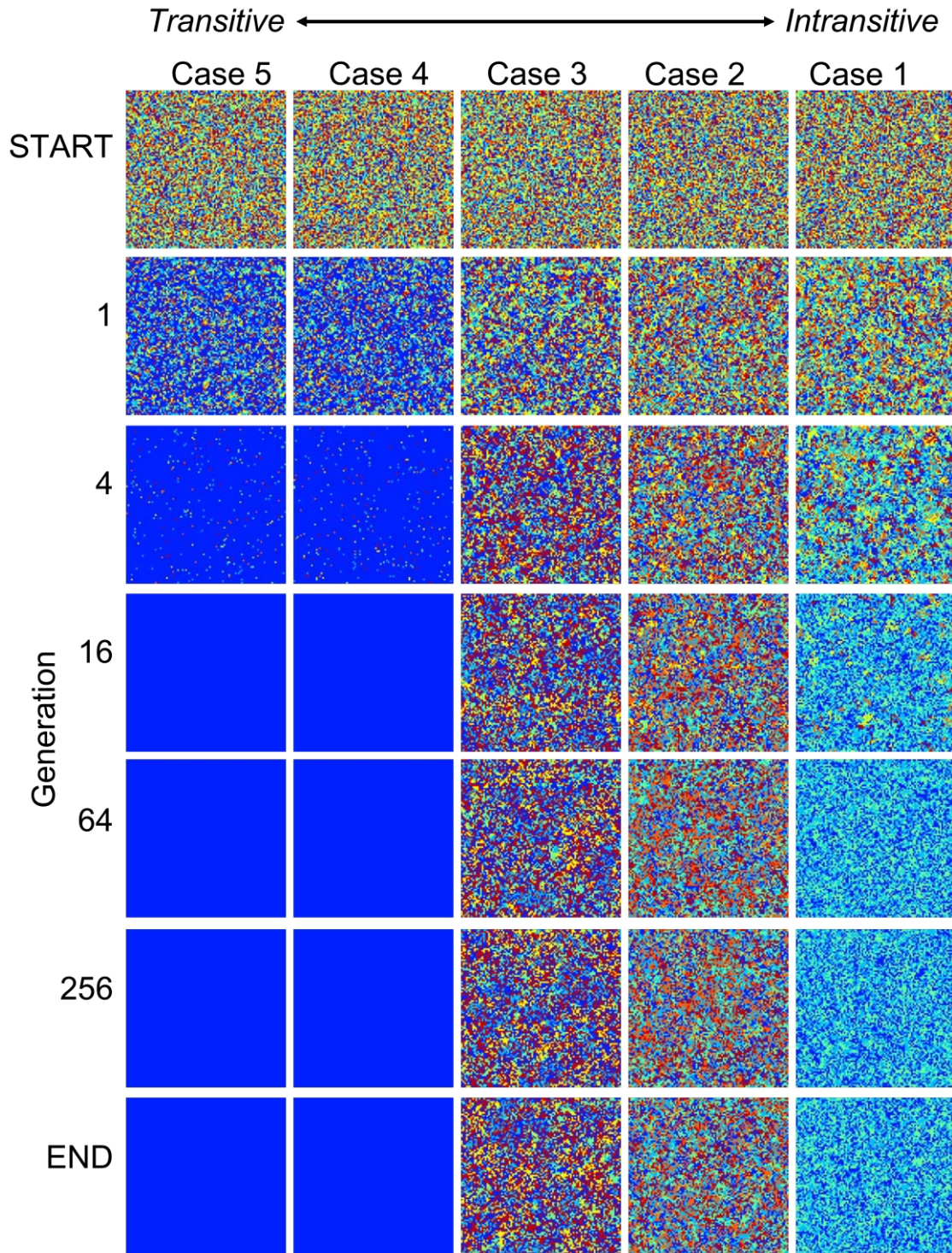


Figure 2: One iteration of the cellular automaton model for $s = 6$ species, for each of the five possible initial values of the index of intransitivity, t (case 5: $t = 1.0$; case 4: 0.75 ; case 3: 0.5 ; case 2: 0.25 ; case 1: 0.0 ; measured at the start of the iteration, before any competition events). The updated 100×100 lattice is shown for the initial conditions (*start*), for every 4^w generations, where w is a whole number between 0 and 4, and for the 500th generation. Note that the most hierarchical cases (5 and 4) quickly descend to monoculture, while species coexistence persists in the more intransitive cases (3, 2, and 1).

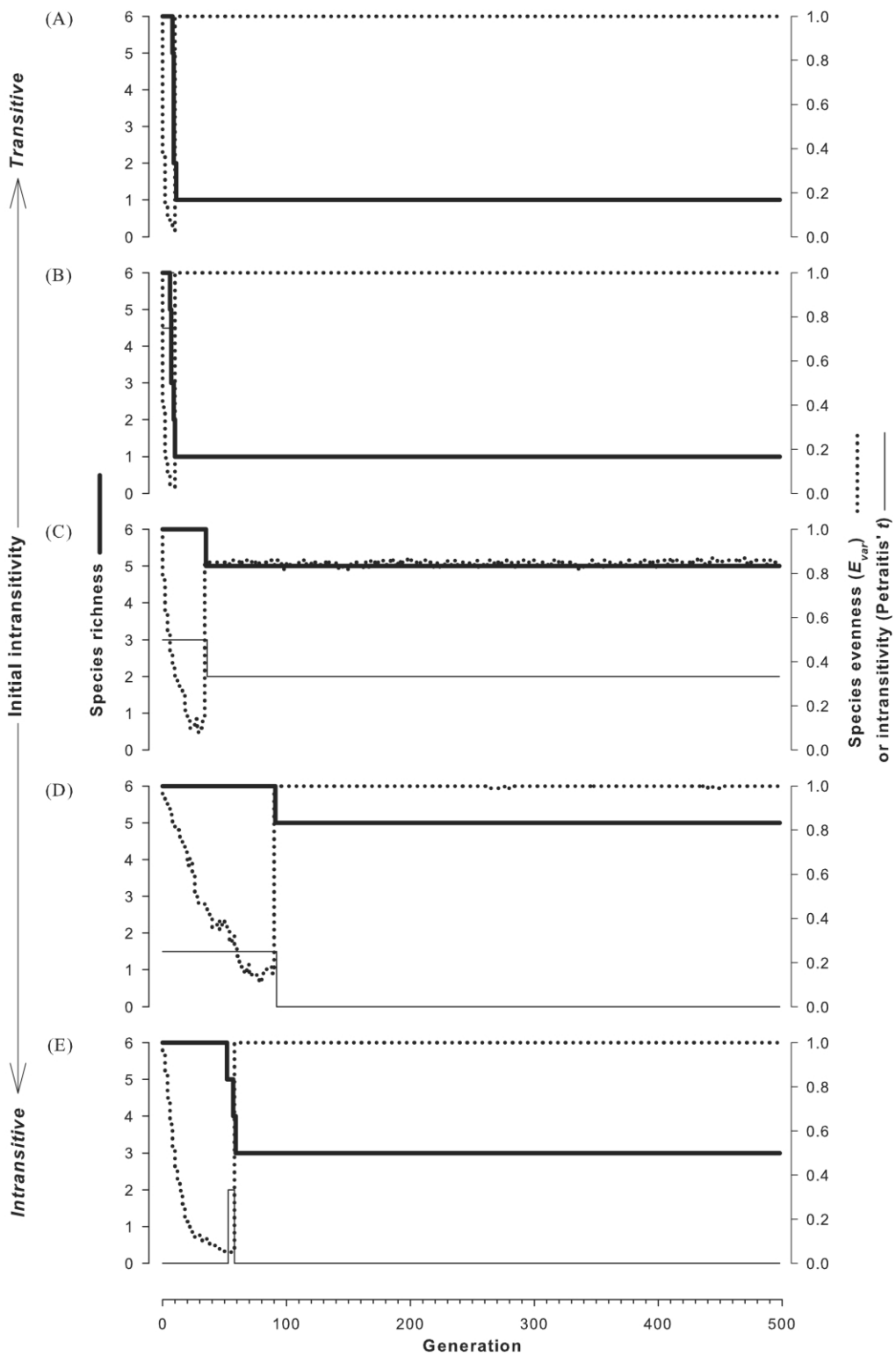


Figure 3: Changes in species richness (*thick solid line*), species evenness (E_{var} ; *dotted line*), and competitive intransitivity (*thin solid line*) across 500 generations, for the same iteration of the cellular automaton model as was shown in figure 2: (A) case 5, initial $t = 1.0$; (B) case 4, initial $t = 0.75$; (C) case 3, initial $t = 0.5$; (D) case 2, initial $t = 0.25$; (E) case 1, initial $t = 0.0$.

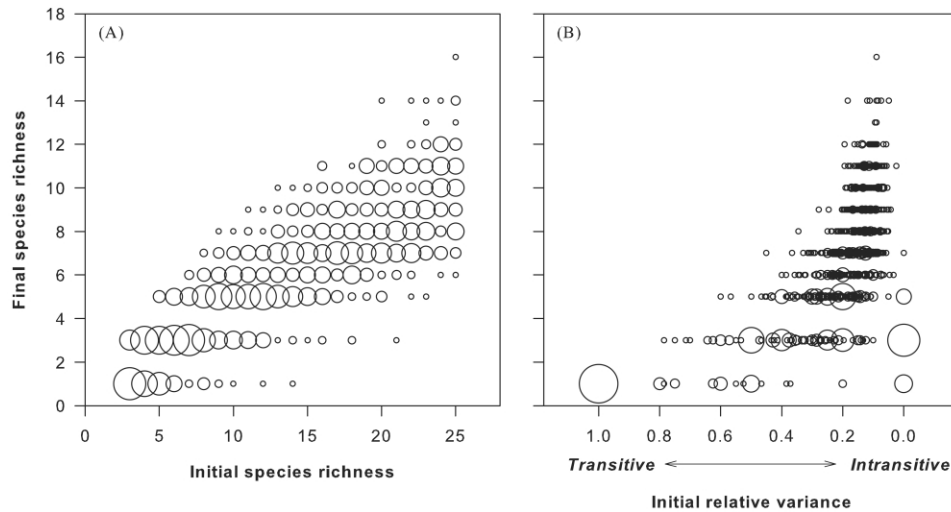


Figure 4: Species coexistence, measured as the number of species remaining after 500 generations, was (A) positively correlated with initial species richness (Spearman partial $\rho = 0.80$, $P < .0001$, $n = 1,150$) and (B) negatively correlated with initial relative variance (i.e., positively correlated with competitive intransitivity; Spearman partial $\rho = -0.41$, $P < .0001$, $n = 1,150$). Symbol areas are proportional to sample sizes. Note the inverted X-axis in B.

in the absence of other mitigating factors (figs. 4, 5). This extends the principle that intransitivity results in winnerless competition from simple low-diversity systems (Durrett and Levin 1998; Huisman and Weissing 1999; Freat and Abraham 2001; Kerr et al. 2002) to more species-rich systems. Additionally, our model highlights the fact that while perfect intransitivity promotes species coexistence, intermediate levels of intransitivity can also play an important role in slowing—if not halting—the process of competitive exclusion (figs. 4, 5). While these intermediate levels of intransitivity may not represent a long-term solution to the maintenance of diversity in communities, they may be responsible for effecting coexistence for situations in which other factors that prevent competitive exclusion are episodic (e.g., many types of disturbance).

In addition to the general finding that intransitivity promotes species coexistence, we observed considerable variation around this relationship in our model communities. For example, in the case of $s = 6$ species, for the single iteration that we examined in detail, the intermediately intransitive community (case 3) actually experienced greater coexistence than the most intransitive community (case 1; figs. 2, 3). While variation in the outcome of competition is an expected consequence of the stochastic nature of simulations, we also found that variation in species coexistence increased with greater levels of intransitivity (figs. 4–6). This suggests that there are other properties of the competitive-outcomes matrix that play a role in determining how intransitivity will affect species co-

existence and are more prevalent at higher levels of intransitivity.

Therefore, further research should consider the finer structure of competitive-outcomes matrices (i.e., their topology) and how this relates to the predictability of species extinctions and coexistence. Important first steps have already been taken. For example, Szabó and Czárán (2001a) considered the effect of interaction topology on competition by examining four communities of $s = 6$ in which each community had the same distribution of wins, losses, and ties (and hence the same relative variance) but a unique arrangement of wins, losses, and ties (and hence a unique topology). Tellingly, this variation in interaction topology had a strong effect on the outcome of competition (e.g., the “defensive alliances” phenomenon; Szabó and Czárán 2001a, 2001b). In another example, Huisman and Weissing (2001a) demonstrated that changes to the details of competition can switch community trajectories between stable coexistence, oscillation, chaos, and competitive exclusion. These examples suggest that the variation in species coexistence that we observed in both our $s = 6$ examples and our full simulations may be partially attributable to unexplored topological variation. Important challenges will lie in examining the importance of other types of topological variation (e.g., see our discussion of “pathway number” in the appendix in the online edition of the *American Naturalist*) and in scaling up the techniques of Szabó and Czárán (2001a, 2001b) and Huisman and Weissing (2001a) to more species-rich communities,

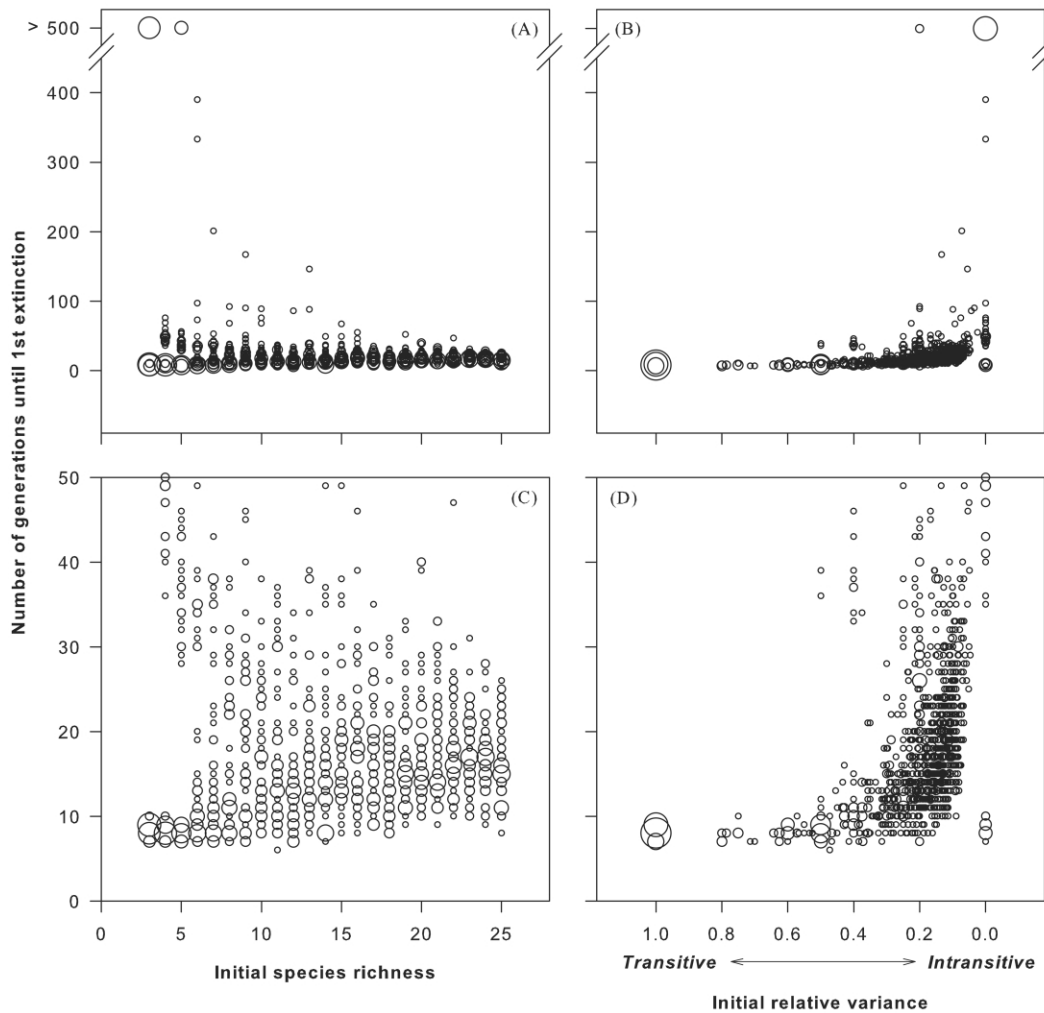


Figure 5: Species coexistence, measured as the number of generations until the first extinction, was negatively correlated with both (A) initial species richness (Spearman partial $\rho = -0.26$, $P < .0001$, $n = 1,150$) and (B) initial relative variance (i.e., positively correlated with competitive intransitivity; Spearman partial $\rho = -0.67$, $P < .0001$, $n = 1,150$). Symbol areas are proportional to sample sizes. For visual clarity, C and D show zoomed-in versions of A and B, respectively. Note the inverted X-axes in B and D.

in which the number of possible topologies increases explosively.

The growing interest in neutral dynamics (Hubbell 2001; Chave et al. 2002; Chave 2004; Tilman 2004; Purves and Pacala 2005) and their potential to contribute to patterns in biodiversity make the study of competitive intransitivity all the more timely. The omission of interspecific competitive interactions from Hubbell's neutral model (Hubbell 2001) is difficult to reconcile with the general finding that competition plays an important role in structuring communities (Grime 1979; Tilman 1982; Schoener 1983; Goldberg and Landa 1991; Gotelli and McCabe 2002), and that, at least where plants are concerned, pairs of species tend to compete asymmetrically

(Weiner 1990; Shipley and Keddy 1994; Schwinning and Weiner 1998) and differ significantly in competitive ability (Keddy and Shipley 1989 and references therein). Competitive intransitivity represents a potential mechanism for "ecological equivalence" whereby species may vary in competitive ability, compete intensely on local scales, and yet still display what appear to be neutral dynamics on larger spatiotemporal scales (Aarssen 2005).

Competitive intransitivity might contribute to ecological equivalence in a second way. Although experiments have shown differences in competitive ability to be the general rule, many studies have found that some species pairs do not significantly differ in competitive ability (e.g., in plants: Wilson and Keddy 1986; in phytoplankton: Passarge et al.

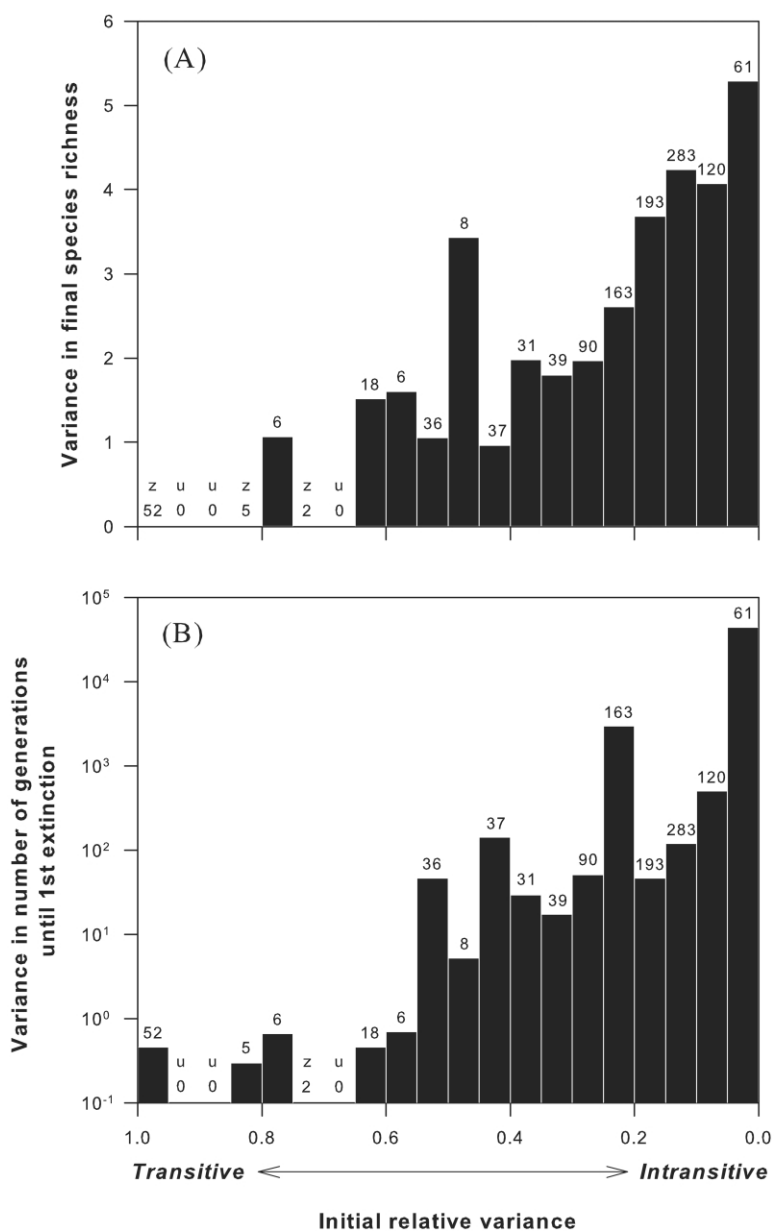


Figure 6: Variance in (A) final species richness and (B) the number of generations until the first extinction for different values of initial relative variance (interval size = 0.05). Numbers above the bars indicate the number of data points used to calculate the variance. Intervals for which bars are absent are marked with “u” to indicate that the variance is undefined, or “z” to indicate that the variance is 0. Note the inverted X-axes in both panels.

2006). Results from these studies can be interpreted in at least two ways: either some species pairs really are competitive equivalents or these competitors are only “equivalent” on average (i.e., at the species level), while varying in competitive ability and competing intransitively at the genotype level (Aarssen 1983, 1989, 1992; Taylor and Aarssen 1990). If the second interpretation is correct, com-

petition within communities may be more intransitive than originally believed. This would suggest an increased role for intransitive competition in communities, given that intransitivity and competitive equivalence at the species level (perhaps driven by genotype-level intransitivity) both contribute to reducing the hierarchical nature of competition.

The notion of intransitively competing genotypes has already been explored in light of the “second paradox of the plankton,” that is, the maintenance of genetic diversity (Hebert and Crease 1980). For example, Czárán et al. (2002) conceptualized the role of genotypic intransitivity in promoting strain diversity in bacteria, and Kerr et al. (2002) found that three strains of *E. coli* could coexist indefinitely because of their “rock-paper-scissors” intransitive arrangement. On the other hand, relaxed (as opposed to fluctuating or cyclic) selection on genotypes due to stage-structured cycles has been implicated as a more likely mechanism for the maintenance of genetic diversity in a microcosm experiment involving a particular suite of *Daphnia* genotypes (Nelson et al. 2005). Notwithstanding this last example, future work should continue to examine how the addition of genotypic intransitivity/species-level competitive equivalence modifies the effects of intransitivity on species coexistence.

Our finding that even intermediate levels of intransitivity can slow competitive exclusion emphasizes the importance of determining just how common intransitively competitive relationships are in natural communities, at both species and genotype levels. Further research should model the outcomes of empirically derived levels of intransitivity and competitive “equivalence” to compare species’ relative abundance distributions generated by intransitivity to those predicted by neutral theory. This would provide a much-needed opportunity to test the hypothesis that neutral patterns may not result strictly from neutral dynamics (Tilman 2004; Purves and Pacala 2005).

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Appendix

The Role of the “Number of Pathways” in Determining Coexistence

We observed considerable variation around the positive coexistence-intransitivity relationship in our model communities (figs. 4–6). This suggests that there are properties of the competitive-outcomes matrix that play a role in determining how intransitivity will affect species coexistence and are more prevalent at higher levels of intransitivity. For example, Petraitis (1979) demonstrated that two competitive-outcomes matrices can have the same level of intransitivity but differ in the number of pathways that change those matrices to a perfectly transitive condition, using an equal and minimum number of competitive reversals (hereafter “number of pathways”). For two communities of equal intransitivity but different numbers of pathways, one might expect the community with more pathways to experience faster and greater species loss, because there are more routes it can take to reach extinction-prone hierarchies. As a preliminary exploration of this possibility, we ran our model for an additional 1,000 randomly generated competitive-outcomes matrices for $s = 6$ species. Unlike the main simulations, we calculated the number of pathways for each competitive-outcomes matrix, along with its intransitivity. (We used Petraitis’s t as our index of intransitivity, rather than relative variance, because it does not take prohibitively long to calculate t when $s = 6$.) The number of pathways did indeed influence species coexistence and was negatively partially correlated with both final species richness and the number of generations until the first extinction (fig. A1). The observed differences in species coexistence between equally intransitive communities with different numbers of pathways—differences that were especially prevalent at higher levels of intransitivity—help to explain the increase in variance that was noted in the main simulations (fig. 6). However, it is important to note that, although the number of pathways was negatively partially correlated with coexistence when examined across the whole range of possible values of intransitivity, within individual levels of intransitivity the relationship between the number of pathways and species coexistence was idiosyncratic (fig. A1). While the number of pathways represents an interesting and important factor influencing coexistence, clearly there are other elements of spatially explicit multispecies competition that cannot be captured using existing indices of intransitivity and numbers of pathways.

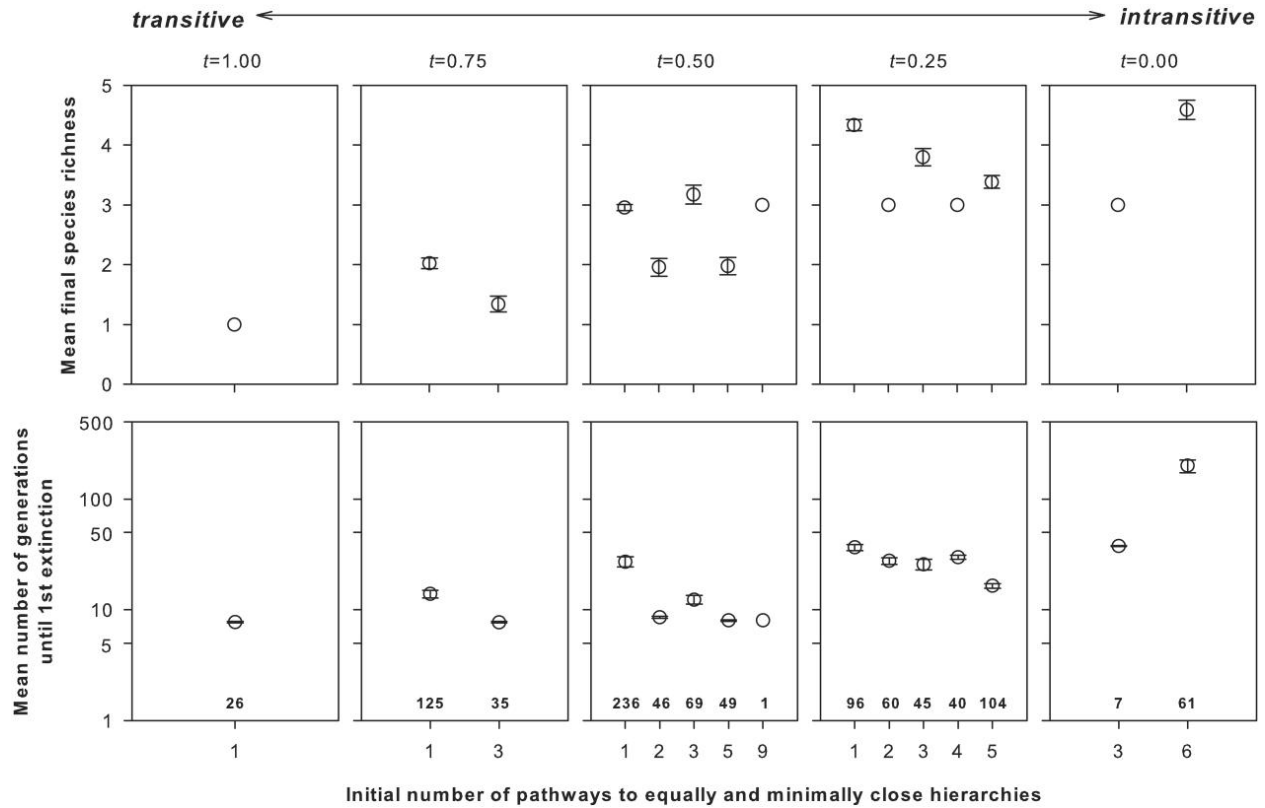


Figure A1: Final species richness (*top row*) and number of generations until the first extinction (*bottom row*) for simulated communities of differing numbers of pathways, across the five possible levels of initial intransitivity (*columns*). In total, there were 1,000 model runs of $s = 6$ species. Symbols represent means \pm SEMs; sample sizes appear under the symbols in the bottom row. The number of pathways was negatively partially correlated with both measures of coexistence (final species richness: Spearman partial $\rho = -0.25$, $P < .0001$, $n = 1000$; number of generations until the first extinction: Spearman partial $\rho = -0.35$, $P < .0001$, $n = 1000$). Within each of the four levels of intransitivity that exhibited variation in the number of pathways, both measures of coexistence varied significantly but idiosyncratically among model communities with different numbers of pathways (Kruskal-Wallis tests, all $P < .05$).