



## Species coexistence, intransitivity, and topological variation in competitive tournaments

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### ABSTRACT

Competitive intransitivity occurs when species' competitive abilities cannot be listed in a strict hierarchy, but rather form competitive loops, as in the game 'Rock–Paper–Scissors'. Indices are useful for summarizing intransitivity in communities; however, as with most indices, a great deal of information is compressed into single number. So while recent ecological theory, experiments, and natural history observations demonstrate that competitive intransitivity can promote species coexistence, the consequence of variation in the 'topology' of competitive interactions that is not accounted for by intransitivity indices is much less well understood. We use a continuous analytical model and two complementary discrete lattice models (one spatially explicit, the other aspatial) to demonstrate that such variation does indeed greatly affect species coexistence. Specifically, we show that although intransitivity indices are good at capturing broad patterns of coexistence, communities with different levels of intransitivity can have equal coexistence, and communities with equal intransitivity can have different coexistence, due to underlying variation in competitive network topology.

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### 1. Introduction

Intransitive competition can be described most easily using the simple analogy of the 'Rock–Paper–Scissors' game in which three strategies compete and each strategy is dominant to just one other: Rock smashes Scissors, Scissors cuts Paper, and Paper covers Rock. This is in contrast to hierarchical or completely transitive competition, which occurs if Scissors cuts Paper, but contrary to the game's tradition, yet perhaps more realistically, Rock smashes both Scissors and Paper. Numerous theoretical models have demonstrated that transitive competition quickly leads to a monoculture of the best competitor (e.g., Rock in the above transitive competition example), while intransitive competition contributes to greater coexistence (Czárán et al., 2002; Durrett and Levin, 1994, 1998; Gilpin, 1975; Huisman et al., 2001; Huisman and Weissing, 1999, 2001a, b; Kerr et al., 2002; Laird and Schamp, 2006, 2008; May and Leonard, 1975; Reichenbach et al., 2007; Szabó et al., 2004; Tainaka, 1988). Thus, intransitivity is a potential mechanism by which competition itself can promote coexistence—in contrast to most coexistence theories which require that competition be mitigated (Chesson, 2000; Huston, 1994; Tokeshi, 1999).

Furthermore, intransitivity has been identified for a wide variety of taxonomic groups, including plants (e.g., Lankau and Strauss, 2007; Shipley, 1993; Taylor and Aarssen, 1990), sessile marine organisms such as bryozoans, ascidians, cnidarians, sponges, and coralline algae (Buss, 1980, 1990; Buss and Jackson, 1979; Jackson, 1983), bacteria (Kerr et al., 2002), and mating strategies in lizards (Sinervo and Lively, 1996; Sinervo et al., 2007). Therefore, intransitive competition may be an important biological mechanism promoting genetic, species, and behavioral diversity in natural systems.

Competition is simplified in three-species models because only completely intransitive or completely transitive competition is possible (e.g., Durrett and Levin, 1994, 1998; Gilpin, 1975; Kerr et al., 2002; May and Leonard, 1975). However, competitive interrelationships can be increasingly complex as more species are considered (e.g., Huisman et al., 2001; Huisman and Weissing, 1999, 2001a, b; Karlson and Jackson, 1981; Laird and Schamp, 2006, 2008). For example, increasing the number of competing species also increases the number of different levels of intransitivity that are possible in a community of competitors (e.g., Laird and Schamp, 2008; Petraitis, 1979). This is true because an intransitive loop requires at least three species (as in Rock–Paper–Scissors), and with more than three species, it is possible to have multiple intransitive loops. Hence, indices of intransitivity (e.g., Bezembinder, 1981; Kendall and Babington Smith, 1940; Laird and Schamp, 2006, 2008; Petraitis, 1979; Slater, 1961), become increasingly continuous as the number of species increases. Moreover, theoretical models have revealed that these

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indices are powerful predictors of species coexistence (Laird and Schamp, 2006, 2008).

One drawback of intransitivity indices, however, is that they abstract a great deal of information regarding competitive relationships among community members (i.e., ‘competitive topologies’) into a single number. This is because the number of possible competitive topologies increases at a much faster rate than the number of species, and hence the number of possible levels of intransitivity (Electronic Supplementary Material 1). Topological variation that is not fully accounted for by intransitivity indices can be visualized by noting that assemblages with equal intransitivity can have different topologies (Fig. 1). Importantly, topological variation that is not accounted for by indices of intransitivity can impact coexistence (e.g., see the discussion of ‘pathway number’ in Laird and Schamp, 2006). In this paper, we use a continuous mean-field model as well as discrete spatial and aspatial lattice models, to demonstrate that although intransitivity indices are good predictors of broad patterns of coexistence, unexplored variation in competition matrix topology influences coexistence for five competing species.

## 2. Methods

### 2.1. Tournament matrices

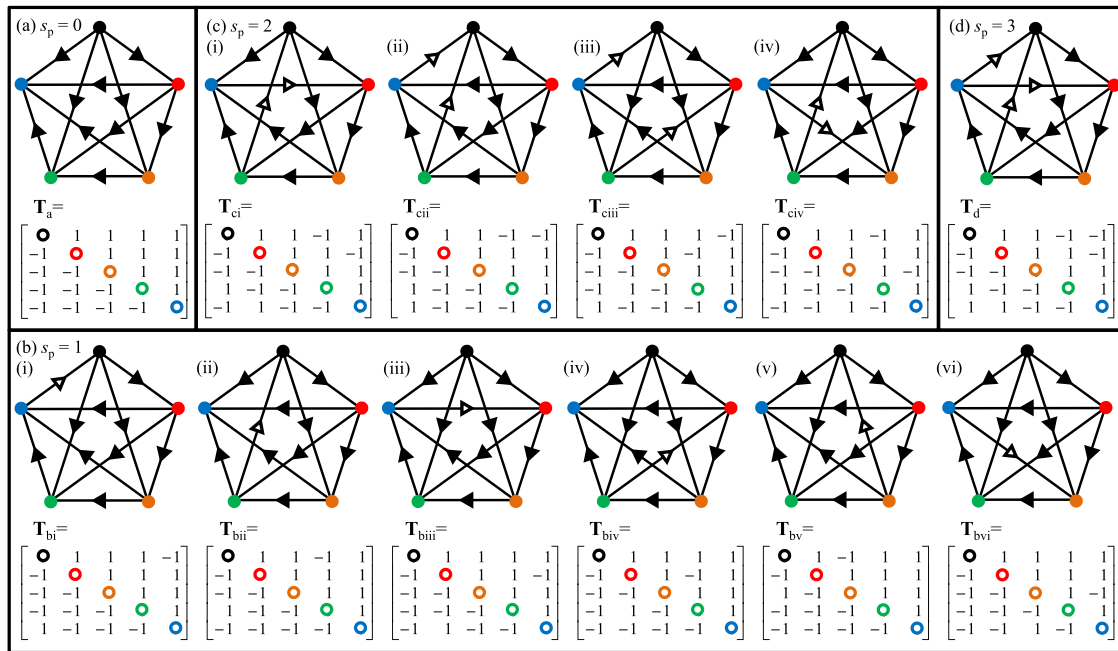
‘Tournament matrices’ describe the competitive relationships for all pairs of species in a community. They are similar to the ‘competitive outcomes matrices’ discussed in Laird and Schamp

(2006, 2008). A tournament matrix for  $s$  species has dimensions of  $s$  rows by  $s$  columns. If the species denoted by row  $i$  outcompetes the species denoted by column  $j$ , position  $(i, j)$  is filled with a ‘1’. Conversely, if the species denoted by row  $i$  is outcompeted by the species denoted by column  $j$ , position  $(i, j)$  is filled with a ‘-1’. If  $i = j$ , position  $(i, j)$  is filled with a ‘0’.

The number of possible tournament matrices increases explosively with the number of species. However, many of these are topologically equivalent (i.e., they are identical unlabeled graphs in the context of graph theory). For instance, the following two matrices are equivalent representations of Rock–Paper–Scissors (‘R–P–S’) competition:

$$\begin{matrix} 0 & -1 & 1 & 0 & 1 & -1 \\ 1 & 0 & -1 & \equiv & -1 & 0 & 1 \\ -1 & 1 & 0 & 1 & -1 & 0 \end{matrix}$$

The left-hand matrix’s rows and columns can be ordered R–P–S, P–S–R, or S–R–P, whereas the right-hand matrix’s rows and columns can be ordered R–S–P, S–P–R, or P–R–S. The matrices are equivalent because one can be converted to another by a simple re-ordering of the rows and columns. Notwithstanding the redundancy of tournament matrices, there are still a huge number of unique tournament matrices as  $s$  becomes large (Goldberg and Moon, 1970). For example, while there are only two unique three-species tournaments (e.g., the traditional and modified Rock–Paper–Scissors games described in Section 1), there are 456 seven-species tournament matrices, and close to a million-billion-trillion 17-species tournament matrices (Electronic Supplementary Material 1).



**Fig. 1.** The twelve unique interaction web diagrams and tournament matrices for five-species communities. Panel names correspond with the ‘tournament names’ in Table 1, the example mean-field predictions in Fig. 2, and the  $x$ -axes of Fig. 3. Species are shown as nodes (circles) and their pair-wise competitive relations are shown as edges (arrows). Arrows point from competitive dominant to subordinate (e.g.,  $\bullet \rightarrow \circ$  means that the species denoted by the black node outcompetes the species denoted by the white node). An example tournament matrix is given for each interaction web: a ‘1’ means the row species outcompetes the column species, a ‘-1’ means the column species outcompetes the row species, and a colour ‘0’ is given when row = column (the 0s also provide the row and column corresponding to the node of the same colour; furthermore, their colours match up with the species in Fig. 2). (a) The ‘hierarchical’ case (Petraitis’  $t = 1$ , minimum number of reversals to convert the matrix to a hierarchy  $s_p = 0$ ; Petraitis, 1979). (b) The six unique manifestations of the ‘moderately intransitive’ case ( $t = \frac{2}{3}$ ,  $s_p = 1$ ). White arrowheads denote the competitive relations that would have to be reversed to convert these networks into the hierarchy given in (a) (for (bi)–(biii), the hierarchy in (a) is the only hierarchy within a single reversal; for (biv)–(bvi), there are two other hierarchies that are equally close—not shown). (c) The four unique manifestations of the ‘strongly intransitive’ case ( $t = \frac{1}{2}$ ,  $s_p = 2$ ). White arrow heads are the same as in (b) (for (ci), the hierarchy in (a) is the only hierarchy within a single reversal; for (cii), (ciii), and (civ), there are, respectively, one, two, and four other equally close hierarchies—not shown). (d) The ‘perfectly intransitive’ case ( $t = 0$ ,  $s_p = 3$ ). White arrowheads are the same as in (b) and (c) (there are four other equally close hierarchies—not shown). All other five-species tournament matrices are reconfigurations of the twelve shown here. Note that Petraitis’  $t$  is equal to one minus the minimum number of reversals needed to convert a tournament to a hierarchy ( $s_p$ ), divided by the maximum possible value of  $s_p$  for communities of a given size (for five-species communities,  $\text{MAX}(s_p) = M = 3$ ; see Table 1).

In this study, we focus on five-species competition. Five-species competition includes four levels of intransitivity (as measured by the index  $t$ ; Petraitis, 1979; Table 1). However, there are 12 unique tournament matrices, examples of which are shown in Fig. 1 (see Table 1 for a summary of the properties of the 12 matrices). Focusing on five-species competition allows us to investigate the consequences of different tournament matrix topologies while keeping analyses tractable.

## 2.2. Mean-field model

We investigated a multi-species extension of Frean and Abraham's (2001) mean-field model of Rock–Paper–Scissors competition (also see Durrett and Levin, 1994). The mean-field model tracks the proportions of competing species assuming that: (1) there are a large number of individuals competing, and (2) contact rates between members of the competing species follow a mass-action rule (i.e., the communities are well-mixed with no spatial structure). The rates of change of the proportions of all species  $i$  are given by the simultaneous differential equations

$$\frac{dx_i}{dt} = \sum_{j=1}^s \mathbf{T}(i, j)x_jx_i \quad \text{for } i = 1, 2, \dots, s \quad (1)$$

where  $x_i$  and  $x_j$  are the proportions of species  $i$  and  $j$ , respectively,  $s$  is the number of species ( $s = 5$  in our analyses), and  $\mathbf{T}$  is the tournament matrix (i.e.,  $\mathbf{T}(i, j) = 1$  if species  $i$  outcompetes species  $j$ ,  $\mathbf{T}(i, j) = -1$  if species  $j$  outcompetes species  $i$ , and  $\mathbf{T}(i, j) = 0$  if  $i = j$ ). We examined the dynamics for each of the twelve unique tournament matrices for five-species competition (Fig. 1). We generally used equal initial relative abundances of [0.2, 0.2, 0.2, 0.2, 0.2], although other starting conditions were also investigated.

**Table 1**

Characteristics of the twelve unique tournament matrices for five-species competition, sorted by  $s_p$ , the minimum number of competitive reversals required to change the tournament matrix into a hierarchy

Tournament name	$s_p^a$	$t^b$	Relative intransitivity <sup>c</sup>	$\rho^d$	$\delta^e$	Pathway number <sup>f</sup>	Score sequence <sup>g</sup>	Predicted richness
a	0	1	0	0	0	1	{0, 1, 2, 3, 4}	1
bi	1	$\frac{2}{3}$	0.6	6	1	1	{1, 1, 2, 3, 3}	3
bii	1	$\frac{2}{3}$	0.4	3	0.6	1	{0, 2, 2, 3, 3}	3
biii	1	$\frac{2}{3}$	0.4	3	0.6	1	{1, 1, 2, 2, 4}	1
biv	1	$\frac{2}{3}$	0.2	1	0.3	3	{0, 2, 2, 2, 4}	1
bv	1	$\frac{2}{3}$	0.2	1	0.3	3	{0, 1, 3, 3, 3}	3
bvi	1	$\frac{2}{3}$	0.2	1	0.3	3	{1, 1, 1, 3, 4}	1
ci	2	$\frac{1}{3}$	0.8	6	1	1	{1, 2, 2, 2, 3}	3
cii	2	$\frac{1}{3}$	0.8	6	1	2	{1, 2, 2, 2, 3}	3
ciii	2	$\frac{1}{3}$	0.8	6	1	3	{1, 2, 2, 2, 3}	5
civ	2	$\frac{1}{3}$	0.6	6	1	5	{1, 1, 2, 3, 3}	3
d	$3 = M$	0	1	6	1	5	{2, 2, 2, 2, 2}	5

Tournament names correspond with the panels of Figs. 1 and 2, and the x-axes of Fig. 3. Four indices of intransitivity are given:  $t$ , relative intransitivity,  $\rho$  and  $\delta$ , as well as the 'pathway number' and 'score sequence' of each tournament. 'Predicted richness' is the number of species predicted by mean-field approximations to experience long-term coexistence (e.g., Fig. 2).

<sup>a</sup>  $s_p$  is equal to Slater's  $i$ , the minimum number of competitive reversals required to change the tournament matrix into a hierarchy ( $s_p$ ; Petraitis, 1979;  $i$ : Slater, 1961).

<sup>b</sup> Petraitis'  $t = 1 - s_p/M$ , where  $M$  is the maximum minimum number of competitive reversals required to change a tournament of a given number of species into a hierarchy (Petraitis 1979). In five-species tournaments,  $M = 3$ .

<sup>c</sup> Relative intransitivity (Laird and Schamp, 2008) is equal to  $1 - \text{relative variance}$  (Laird and Schamp, 2006). Additionally, relative intransitivity is equal to  $1 - \zeta$  (where  $\zeta$  is Kendall and Babington Smith's coefficient of consistence; Kendall and Babington Smith, 1940).

<sup>d</sup> Bezembinder's  $\rho$  is the rank of the 'cycle matrix' (Bezembinder, 1981).

<sup>e</sup> Bezembinder's  $\delta$  is the proportion of pairwise competitive outcomes that are embedded in a cycle (Bezembinder, 1981).

<sup>f</sup> Pathway number is the number of different hierarchies within  $s_p$  competitive reversals of a given tournament (Laird and Schamp, 2006). Pathway number is equal to Slater's  $j$  (Slater, 1961).

<sup>g</sup> Score sequence is the number of competitors that each species outcompetes, reported in ascending order.

## 2.3. Lattice models

The lattice models are described in detail in Laird and Schamp (2006, 2008). Briefly, five-species communities were seeded randomly and independently on a  $100 \times 100$  cell lattice with periodic boundaries. Initially, the probability of each cell being occupied by a given species was equal to 0.2. During each time step, a focal cell was chosen at random and the individual occupying it competed either against its eight nearest neighbors in its  $3 \times 3$  cell neighborhood (i.e., 'local competition'), or against eight other individuals chosen randomly from the lattice (i.e., 'global competition'). If one of these eight competitors was competitively dominant to the focal individual, the focal individual was replaced by a new individual of the superior competitor. If more than one of the eight competitors was dominant, replacement was random and proportional to the relative abundance of the superior competitors (i.e., their relative abundance among the eight competitors, not in the lattice at large). Ten-thousand competition events were defined as one generation, so that on average, every cell served as the focal cell once per generation. For each of the twelve unique tournament matrices for five-species competition (Fig. 1), we ran 50 global and 50 local model replicates. For each replicate, we recorded short-term coexistence (defined as the number of generations until the first extinction) and long-term coexistence (defined as the number of species remaining after 500 model generations).

## 3. Results and discussion

### 3.1. Mean-field model

The mean-field model results show that for some five-species tournament matrices, no coexistence is possible, and communities

quickly become monocultures (e.g., Fig. 2a). However, for other tournament matrices three- or even five-species coexistence is possible (e.g., three species: Fig. 2bi, bv, ci; five species: Fig. 2ciii, d). The full results of the predicted long-term coexistence for communities in which all five species start with a relative abundance of 0.2 are given in Table 1. Although intransitivity indices are excellent predictors of species coexistence (Laird and Schamp, 2006, 2008), there is still unexplained variation in coexistence. For example, of the six possible ‘moderately intransitive’ tournament matrices for which Petraitis’ (1979) index of intransitivity  $t = \frac{2}{3}$ , three matrices result in three-species coexistence (Table 1bi, bii, bv), while the other three result in monocultures (Table 1biii, biv, bvi). Moreover, it is possible to have equal coexistence in competitive communities with different levels of intransitivity. For example, communities that descend to monoculture include not only the hierarchical case (Table 1a), but also half of the communities for which  $t = \frac{2}{3}$ . Additionally, communities that support three coexisting species are split between those with  $t = \frac{2}{3}$  (Table 1bi, bii, bv) and  $t = \frac{1}{3}$  (Table 1ci, cii, civ). Thus, the mean-field model results demonstrate that the fine details of competitive topologies can be very important in determining species coexistence when interactions are global, such as in well-mixed aquatic communities (Huisman et al., 2001).

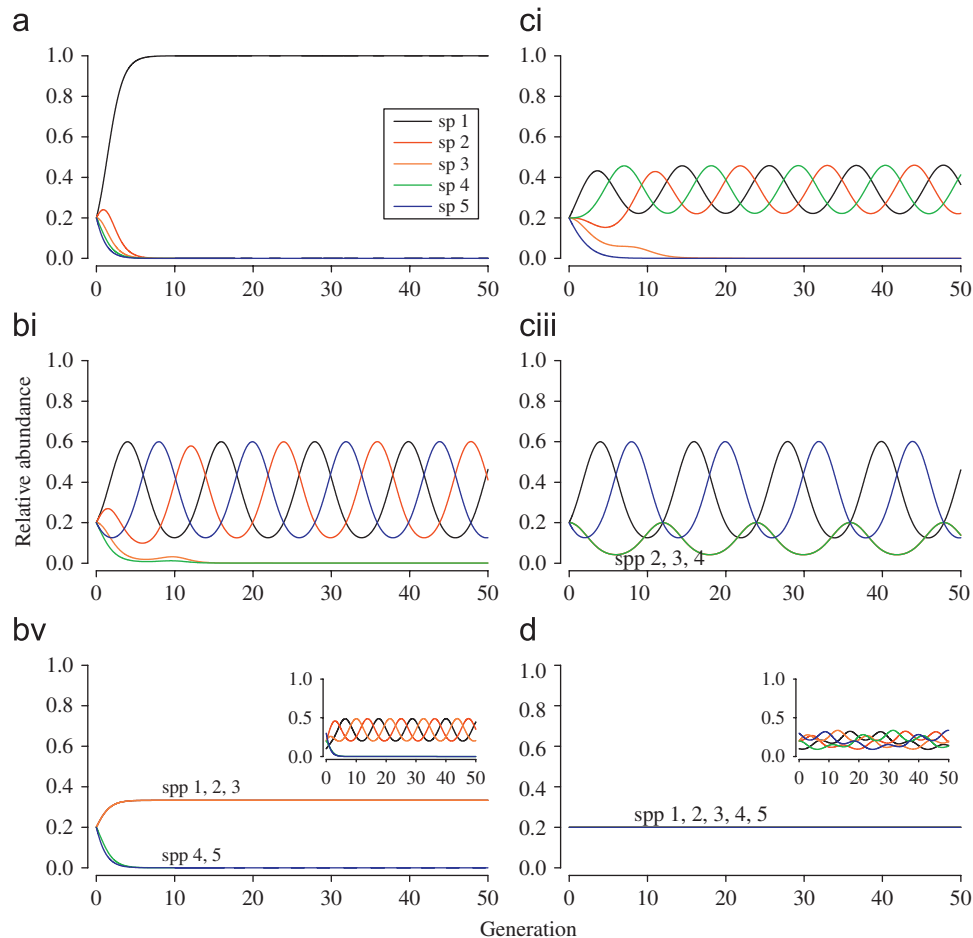
Importantly, other indices such as relative intransitivity (Laird and Schamp, 2008), which is equivalent to  $1 - \zeta$  (Kendall and Babington Smith, 1940),  $\rho$  and  $\delta$  (Bezembinder, 1981), and pathway number (Laird and Schamp, 2006), which is equivalent

to Slater’s  $j$  (Slater, 1961), were also unable to explain all of the observed variation in coexistence for five-species tournament matrices (see Table 1). This further supports our conclusion that topological variation in competition external to intransitivity can contribute to patterns of coexistence.

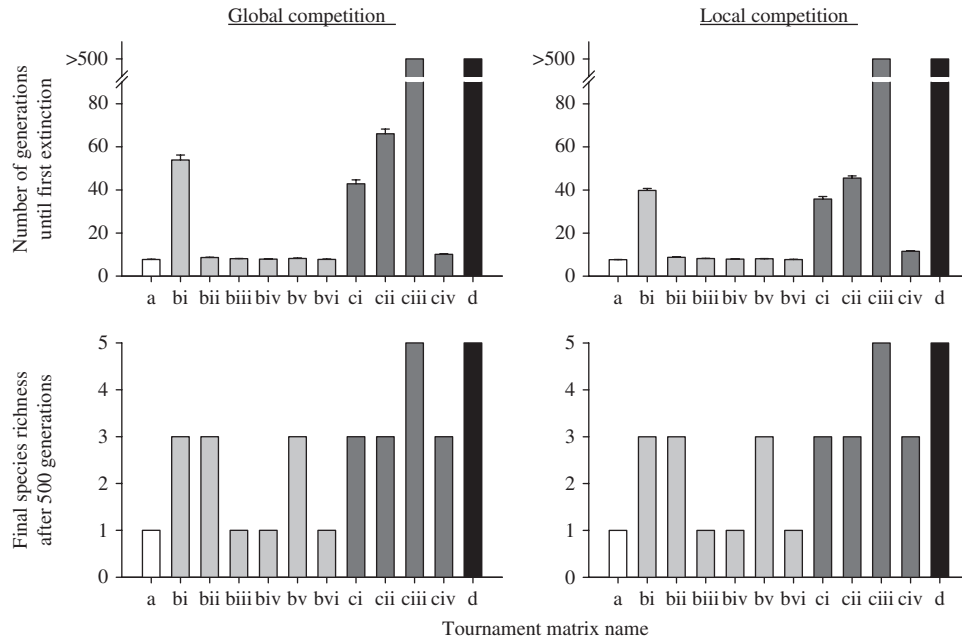
### 3.2. Lattice models

Electronic Supplementary Materials 2 and 3 show example lattice model runs for the same six tournament matrices that are shown in Fig. 2. Generally, the dynamics are similar to the mean-field model results, in that the same species coexist and the same species go extinct. However, a major difference between the mean-field results and the lattice model results is that the oscillations that are observed in the mean-field model are strongly suppressed in the lattice models. In our lattice models, the focal competitor interacts with eight other competitors, and thus has as many as eight chances of being replaced per competition event, while in the mean-field model competition events effectively occur within pairs of individuals (i.e., one chance of replacement per competition event; Frean and Abraham, 2001). Hence, fluctuations in abundance are dampened in the lattice models relative to the mean-field model.

A summary of the results of the lattice models is shown in Fig. 3. The results of global and local competition are the same in terms of long-term coexistence (i.e., number of species remaining



**Fig. 2.** Mean-field model predictions for six of the twelve unique five-species competitive tournament matrices. Panel names correspond with the ‘tournament names’ in Table 1 and the tournament matrices in Fig. 1. Line colors match the colors of species in Fig. 1. The main panels show the dynamics of the relative abundances of species 1–5 with starting conditions of [0.2, 0.2, 0.2, 0.2, 0.2]. Insets show that oscillatory dynamics are possible for the tournaments in the respective main panels: insets of (bv) and (d) show the dynamics when the starting conditions are [0.1, 0.2, 0.2, 0.2, 0.3]. Species names are indicated where lines wholly overlap.



**Fig. 3.** Lattice model results for the twelve unique tournament matrices for five species. Labels in the x-axes correspond with the ‘tournament names’ in Table 1 and the tournament matrices described in Fig. 1. Bars represent the means of 50 model runs. Similarly shaded bars represent tournament matrices of equal intransitivity as measured with Petraitis’ index (1979) (see Table 1). Error bars represent 1 SEM (bars without error bars had no variation). The four panels show short-term coexistence (number of generations until first extinction; *top row*) and long-term coexistence (number of species remaining after 500 model generations; *bottom row*) for global competition (*left column*) and local competition (*right column*). Note that the outcome of the mean-field model correctly predicted long-term species coexistence in both global and local competition (compare the results in the *bottom row* with the last column of Table 1).

after 500 generations; Fig. 3: *bottom row*). Further, the mean-field model correctly predicts the number of species that experience long-term coexistence in both lattice models (compare the *bottom row* of Fig. 3 with the leftmost column of Table 1). However, for some tournament matrix topologies, global competition leads to slightly greater short-term coexistence (i.e., more generations passed until the first extinction event; Fig. 3: *top row*: bi, ci, cii), a trend that is reversed when more than five species are included in the analysis (Laird and Schamp, 2008).

Thus, the lattice model results confirm the mean-field model results: in local and global competition, unexplained variation in competitive topology is important in determining short- and long-term species coexistence.

#### 4. Conclusions

Our results show that topological variation in competitive tournaments that is not captured by intransitivity indices can affect species coexistence in competitive communities. Therefore, the number of reversals in a competitive tournament matrix, which is closely related to intransitivity indices, while important, misses important variation related to reversal location within tournament matrices. Specifically, communities with different levels of intransitivity can have equal coexistence, and communities with equal intransitivity can have different coexistence. This conclusion is independent of the particular intransitivity index being used.

Our findings have important implications for biological systems, especially those in which intransitive competitive relationships have been identified (e.g., Buss, 1980, 1990; Buss and Jackson, 1979; Jackson, 1983; Kerr et al., 2002; Lankau and Strauss, 2007; Shipley, 1993; Sinervo and Lively, 1996; Sinervo et al., 2007; Taylor and Aarssen, 1990). Except for the hierarchical case, all topological variation that we explore results from at least some groups of species within a community interacting intransitively. Thus, identifying variation in competitive tournament

matrix topology will require the same empirical approach used to identify intransitivity (i.e., determining the competitive outcomes within all species pairs in a community). It is clear from our results that competitive topologies can vary in their impact on species coexistence over and above how they are summarized by indices of intransitivity. Thus, the details of *which* species form intransitive loops—and not merely how many do—will be important in understanding the potential contribution of competitive interactions to sustained coexistence.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2008.09.017.

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