Competitive intransitivity, population interaction structure, and strategy coexistence

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HIGHLIGHTS

- Intransitive competition (as in the game rock–paper–scissors) promotes coexistence.
- Spatial structure can enhance intransitivity-mediated coexistence.
- We model intransitivity on spatial, small-world, and regular random graphs.
- Coexistence that occurs in spatial lattices is inhibited as network disorder grows.
- Threshold disorder for monoculture is positively related to population size.

ARTICLE INFO

ABSTRACT

Intransitive competition occurs when competing strategies cannot be listed in a hierarchy, but rather form loops—as in the game rock–paper–scissors. Due to its cyclic competitive replacement, competitive intransitivity promotes strategy coexistence, both in rock–paper–scissors and in higher-richness communities. Previous work has shown that this intransitivity-mediated coexistence is strongly influenced by spatially explicit interactions, compared to when populations are well mixed. Here, we extend and broaden this line of research and examine the impact on coexistence of intransitive competition taking place on a continuum of small-world networks linking spatial lattices and regular random graphs. We use simulations to show that the positive effect of competitive intransitivity on strategy coexistence holds when competition occurs on networks toward the spatial end of the continuum. However, in networks that are sufficiently disordered, increasingly violent fluctuations in strategy frequencies can lead to extinctions and the prevalence of monocultures. We further show that the degree of disorder that leads to the transition between these two regimes is positively dependent on population size; indeed for very large populations, intransitivity-mediated strategy coexistence may even be possible in regular graphs with completely random connections. Our results emphasize the importance of interaction structure in determining strategy dynamics and diversity.

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1. Introduction

A main question in community ecology is how species can coexist despite differences in competitive ability (Chesson, 2000; Huston, 1994; Hutchinson, 1959; Tokeshi, 1999; Wilson, 1990, 2011). Many mechanisms have been proposed, most of which invoke exogenous factors that lessen the impact of competition. Here, we deal with a mechanism that is endogenous to the competitive system itself: competitive intransitivity (Gilpin, 1975; May and Leonard, 1975). Using simulation models, we consider intransitive competition and coexistence among 'strategies', a general term referring to any entities (most commonly species, but also including physiological, behavioral, life-historical, and even ideological variants or strains) that compete, and in doing so, have the potential to exclude one another from their environment.

Transitive competition occurs when strategies can be listed in a strict hierarchy in which strategies higher on the list outcompete those lower on the list, but not vice versa. Transitive competition appeals to the intuition: If strategy A outcompetes strategy B, and B outcompetes C, it makes intuitive sense that A outcompetes C. However, this is not necessarily the case. The simplest counter-example, and, thus, the simplest example of intransitive competition,

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is the game of rock–paper–scissors, in which Paper beats Rock, Rock beats Scissors, and Scissors beats Paper. In populations composed of these three strategies, cyclic dynamics occur, leading to the potential for the coexistence of all three, provided the fluxes in the cycles are not too strong (e.g., Gilpin, 1975; May and Leonard, 1975; Vandermeer, 2011). Rock–paper–scissors and its descendants are fundamentally frequency-dependent phenomena, and the study of intransitive competition and its effects on coexistence are important facets of evolutionary game theory (Hofbauer and Sigmund, 1998; Maynard Smith, 1982; Nowak, 2006; Sigmund, 2010). Extending beyond theoretical considerations, real-world empirical examples of intransitivity-mediated coexistence now span many branches of the tree of life, including within or among bacteria (Kerr et al., 2002; Kirkup and Riley, 2004; Nahum et al., 2011), vertebrate (Bleay et al., 2007; Sinervo and Lively, 1996; Sinervo et al., 2007) and invertebrate animals (Buss, 1976, 1980; Buss and Jackson, 1979; Dunstan and Johnson, 2005; Jackson and Buss, 1975; Rubin, 1982), coralline algae (Buss, 1976, 1980; Buss and Jackson, 1979), plants (Lankau and Strauss, 2007; Taylor and Aarssen, 1990), and possibly phytoplankton (Huisman and Weissing, 2001b) and yeasts (Paquin and Adams, 1983). Intransitivity also bears upon important issues in human decision-making procedures (Kendall and Babington Smith, 1940; May, 1954; Tversky, 2004), including voting systems (Arrow, 1950; Hughes, 1980; Riker, 1961).

Although classic theory and simulation papers typically deal with three-strategy intransitivity (e.g., Czárán et al., 2002; Durrett and Levin, 1998; Frean and Abraham, 2001; May and Leonard, 1975; Neumann and Schuster, 2007; Schreiber and Killingback, 2013; Szabó et al., 2004; Tainaka, 1988), and many of the empirical examples above involve variants of rock–paper–scissors (e.g., toxic, resistant, and susceptible strains of *Escherichia coli* (Kerr et al., 2002); orange, yellow, and blue chromo-behavioral morphs of side-blotched lizards (Sinervo and Lively, 1996)), the study of the relationship between competitive intransitivity and coexistence can be generalized to more strategy-rich communities (Gilpin, 1975; Huisman and Weissing, 1999, 2001a,b; Huisman et al., 2001; Karlson and Jackson, 1981; Laird and Schamp, 2006, 2008, 2009). This reflects the facts that (a) in many systems, multi-strategy communities are common (e.g., multi-species communities in biological systems or multiple ideologies in the socio-political sphere), and (b) intransitivity readily results from typical traits of these multi-strategy communities, such as trade-offs during exploitation competition (Huisman and Weissing, 1999, 2001a,b; Huisman et al., 2001) and allelopathy (Kerr et al., 2002; Lankau and Strauss, 2007). When this generalization is made, the transitive-intransitive dichotomy gives way to a series of inter-mediately intransitive competition scenarios that becomes increasingly continuous as the number of strategies grows. The level of intransitivity across this continuum can be quantified using an index (Bezembinder, 1981; Kendall and Babington Smith, 1940; Laird and Schamp, 2006, 2008; Petraitis, 1979; Slater, 1961), making it straightforward to examine quantitatively the relationship between strategy coexistence and intransitivity. As would be expected by extrapolating the lesson of three-strategy coexistence, competitive intransitivity also promotes strategy coexistence when more than three strategies are involved (e.g., Allesina and Levine, 2011; Karlson and Jackson, 1981; Laird and Schamp, 2006, 2008, 2009; Rojas-Echenique and Allesina, 2011; but see Vandermeer and Yitbarek, 2012 for a counterexample). Thus, intransitivity may play an important role in maintaining diversity in communities of varying types.

The simplest intransitivity models within evolutionary game theory have no interaction structure; rather, they behave according to mean-field assumptions, whereby strategies embedded in large, well-mixed communities interact according to their relative abundances and the principle of mass action (e.g., Allesina and Levine, 2011; Frean and Abraham, 2001; Gilpin, 1975; May and Leonard, 1975). Allesina and Levine (2011) provide an effective means to deal with these models and predict the outcome of competition. However, paralleling the rising interest in the effect of interaction structure in evolutionary game theory in general (particularly in models designed to understand the evolution of cooperation, and, specifically, how cooperators and defectors can coexist: Hauert, 2001, 2002, 2006; Hauert and Doebeli, 2004; Laird, 2011, 2012, 2013; Laird et al., 2013; Lieberman et al., 2005; Nowak and May, 1992, 1993; Nowak et al., 1994a,b; Szabó and Tőke, 1998; Szolnoki et al., 2008), there is a proliferation of studies of intransitive competition in which mean-field assumptions are relaxed (e.g., Durrett and Levin, 1998; Frean and Abraham, 2001; Károlyi et al., 2005; Laird, 2014; Reichenbach et al., 2007; Schreiber and Killingback, 2013; Szabó et al., 2004; Szolnoki and Szabó, 2004; Tainaka, 2001; Zhang et al., 2009). The general lesson is that variation in interaction structure can modify greatly the outcome of competition in intransitive systems.

Spatial structure, whereby individuals interact preferentially (or solely) with their nearest neighbors, is one of the main types of interaction structure that has been modeled in the context of intransitivity-mediated strategy coexistence (Durrett and Levin, 1998; Frean and Abraham, 2001; Kerr et al., 2002; Laird and Schamp, 2006, 2008, 2009). This type of structure is particularly relevant in biological systems whose members are largely sessile and confined to a two-dimensional substrate (e.g., biofilms (Kerr et al., 2002); encrusting benthic invertebrates (Dunstan and Johnson, 2005; Wootton, 2001)). Generally speaking, simulations predict that spatially explicit interactions enhance intransitivity-mediated coexistence (e.g., Durrett and Levin, 1998; Frean and Abraham, 2001; Kerr et al., 2002; but see Laird and Schamp, 2008; Rojas-Echenique and Allesina, 2011). This prediction is supported by key experimental data (e.g., Kerr et al., 2002).

The advent of evolutionary graph theory (Lieberman et al., 2005; Nowak, 2006; Perc et al., 2013; Szabó and Fáth, 2007) provides a framework whereby individuals interacting in arbitrarily structured populations can be studied. In this manner, spatial structure becomes a special case of interaction topology. As with spatial extensions of evolutionary game theory, more general graph-theoretical extensions are strongly influenced, in terms of approach, by recent models of the evolution of cooperation (Du et al., 2009; Hadzibeganovic et al., 2012; Lieberman et al., 2005; Lima et al., 2009; Nowak, 2006; Pacheco et al., 2006; Szolnoki and Perc, 2009; Szolnoki et al., 2008; Wang et al., 2006). In evolutionary graph theory, individuals interact with a subset of the population/community to which they belong, though not necessarily with those that are spatially close. In terms of intransitivity-mediated strategy coexistence, evolutionary graph theory is most relevant in humans and other species in which the existence of social networks can lead to complex population-level interaction structures. Additionally, there are other systems (biological, social, and technological) where interactions on graphs or networks are the norm (Watts and Strogatz, 1998). Finally, even in systems where aspatial interaction graphs are unlikely, modeling the outcome of interactions on such graphs may provide a point of contrast—a tool with which salient aspects of more realistic interaction structures can be examined in detail (e.g., Laird, 2014).

Szabó et al. (2004) and Szolnoki and Szabó (2004) consider the rock–paper–scissors game along a continuum of regular, small-world networks (Watts and Strogatz, 1998) ranging from spatial lattices to regular random graphs (also see Kuperman and Abramson, 2001; Laird, 2014; Ying et al., 2007). They show that by increasing quenched randomness (profitably thought of as an inverse measure of inherent spatial structure), disparate parts of the network become synchronized, leading to a Hopf bifurcation at which the strategy frequency dynamics transition from a