



Symmetry breaking in cyclic competition by niche construction



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ABSTRACT

Niche construction theory, which portrays organisms as active agents that modify their environment rather than mere passive entities selected by their environment, has received increasing attention in ecology and evolutionary biology. Here, we investigate the ecological consequences of niche construction in the system of three cyclically competing metapopulations, engaging a rock–scissors–paper game. Using cellular automata, we detected a variety of dynamic behaviors, including damped oscillation, periodical fluctuation and stage equilibrium, and the system transformed from disorder to order with gradually increasing niche-constructing intensity. Increasing niche-constructing intensity of a species, counterintuitively, reduced its own occupancy, but increased that of its inferior competitor. These species displayed interesting ripples in the two-dimension lattice space, with the pattern sensitive to the symmetry of competition intensity and other vital rates. Spatial heterogeneity induced by niche construction, together with the competition hierarchy, formed a stable and fixed range for each species with clear boundaries. Our results highlighted the necessity of investigating the adaptive dynamics of niche constructing traits to better understand the eco-evolutionary consequence of niche construction.

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1. Introduction

Niche construction, where organisms can actively modify their environment rather than being passively selected by the environment, is a recent concept in evolutionary ecology [1–5]. It refers to the capacity of organisms to construct, modify, and select important components of their environment to meet their niche demand, such as through building nests and burrows, releasing chemicals and nutrients, which consequently modify both abiotic and biotic forces of natural selection in the local environment. In doing so, niche construction could generate a feedback between environmental processes and eco-evolutionary ones [4,6–10]. Niche construction could, arguably, be an evolutionary process by its own right, rather than a mere product of evolution [11–13]. Nonetheless, niche construction can be considered equivalent to ecosystem engineering at the ecological time scale, often through modifying the flow of energy and matters in ecosystems [2,3,14].

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To date, the majority of theoretical models for describing the dynamics of niche construction have confirmed that niche construction can remarkably affect the dynamics and distribution of involved species [2,3,8–10,15,16]. For example, Hui et al. [15] found that organism–environmental feedbacks from niche construction can profoundly affect the outcome of competition and the maintenance of biodiversity in metapopulations, mainly through forming self-organized environmental heterogeneity and range-limited species distributions. Han and Zhang [16] expanded on Tilman’s multi-species competition model by incorporating niche construction component to illustrate that niche construction also affects the ecological order of metapopulation, i.e. the sequence of populations’ occupy proportion of habitat. In a model of two consumers that compete for one limiting resource but consumed by one common predator, niche construction can either generate net interspecific facilitation or strengthen interspecific competition via altering the balance between intraspecific and interspecific competitive effects [3]. Through rescuing the depleting resource, niche construction can also foster species coexistence [3]. Various processes of niche construction can also lead to diverse spatial distributions of species such as spiral wave, spiral-broken wave and circular wave [9], and it can even restrain gene flows along environmental gradients via forming fitness valleys [10].

Cyclic population dynamics, as manifested in the rock–scissors–paper game, have been previously studied by many for elucidating the mechanisms of biodiversity and self-organized patterns using lattice models and partial differential equations (e.g., [17–38]). Results from most these models show the emergence of self-organized spatial distribution of species and complex patterns of coexistence, such as entangled rotating spiral waves (e.g. [17,18,22–24,35,38]), remarkable target-wave [25,38], chaotic patches [26] and phase transition of suddenly appearing large-scale fluctuations [20,36]. These various outcomes can be explained by the topological shape, spatial structure, interaction range and rate, as well as species (or player) numbers in the ecological or evolutionary network [30]. Reichenbach et al. [23] have analyzed the spiral waves from low mobility and computed the wavelength and spreading velocity of spirals. Evidently, biodiversity in a community experiencing cyclic competition depends heavily on the difference between species’ mobility (or invasion rate) [26,30]. Protection spillovers where species *A* indirectly facilitates species *B* via suppressing the natural enemies of *B*, may also change the dynamics of cyclic dominance fundamentally in structured populations, which could underpin the phenomenon of microbial coexistence [38]. A recent study on the population dynamics of three cyclically competing species in a two-dimensional turbulent fluid system sheds new insight to how turbulent transportation affects ecosystem structure in communities without a clear competition hierarchy [32]. It has also been widely observed in cyclic game models of the dominance of inferior species (e.g., [17–19]). Studies on an extension of the rock–paper–scissors game, named the finger game [27] or rock–paper–scissors–lizard–Spock (RPSLS) game [29,36] which includes five species along a cyclic hierarchy, also confirmed that a large number of species and high mobility can jeopardize biodiversity maintenance and potentially lead to diverging fluctuations under strong mixing [36]. In a six-species predator–prey cyclic system, an unexpected non-monotonous dependence of alliance survival on special heterogeneous invasion rates, even with the Gaussian noise, was revealed [33,34]. The extinction time of a well-mixed four cyclically competing species was estimated to have correlated linearly with the system size, and the probability distribution of extinction time takes roughly the shape of a shifted exponential distribution [28,31]. Szolnoki et al. [37] showed that the transition from pairwise to group interactions can decelerate or even reverse the direction of invasion between competing players. Time-dependent factors were also found important for cyclic system; different capacities of learning by players in the spatial prisoner’s dilemma game offer alternative ways for the persistence of cooperators [35].

Cyclic competition can also emerge spontaneously in evolutionary public goods games with volunteers [39], peer punishment [40], pool punishment [41,42], reward [43,44] and reciprocity [45]. A spatial public goods game generally includes three elementary strategies: to defect, to reward and to punish. Other deformations of this classic setup have resulted in rich dynamic behaviors [41,42,45]. For example, defection remains viable when the rewarding is costly. Moderate rewards may promote cooperation better than big rewards, especially if the return from cooperative contributions is low [44]. Moreover, regardless of the return ratio which governs the public goods game, punishment in particular are more effective in deterring defection than the combined strategy of punishment, reward or defection [45]. Indeed, this topic has received a comprehensive review recently (see [30]).

Symmetry, meaning uniformity or invariance in patterns or structures, is often appealing and inspiring in natural systems [46]. Symmetry breaking is the process by which the uniformity is broken so to generate a more structured and improbable state in the focal system [47]. In general, increasing levels of broken symmetry in systems are often associated with increasing complexity and functional specialization of system components [46], and are true in biology across all system scales, from the macromolecules https://en.wikipedia.org/wiki/Symmetry_breaking_and_cortical_rotation-cite_note-3 to tissues and organs (see [48–55]). In ecological systems, symmetry breaking has received wide attention especially under the framework of cyclic competition, partly because the asymmetric scenarios can be diverse. For instance, if the dispersal rates of all species are close/similar to each other, the coexistence takes the form of spiral waves or target waves [22]. The spiral dynamics, however, do not appear if the species have unequal mobility. The greater the disparity between dispersal rates, the shorter the distance to the origin at which the spiral waves break down, and the dynamics begin to resemble several tangled spirals, eventually without forming spirals [26,27]. In systems of marine phytoplankton [56] and atmospheric microbes [57], advection and diffusive transportation in cyclic competition can further interact with the environment and form a complex interplay of diverse factors dictating symmetry breaking [32].

Here, we investigate the ecological consequences of niche construction in three cyclically competing species. Competition among these three species resembles the game of rock–scissors–paper (as in Zhang et al. [58]). The rock species *R* can invade the habitat patches occupied by the scissors species *S*; the scissors species *S* can invade the habitat patches occupied

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