Article

Spatial distributions of niche-constructing populations

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Abstract

Niche construction theory regards organisms not only as the object of natural selection but also an active subject that can change their own selective pressure through eco-evolutionary feedbacks. Through reviewing the existing works on the theoretical models of niche construction, here we present the progress made on how niche construction influences genetic structure of spatially structured populations and the spatial-temporal dynamics of metapopulations, with special focuses on mathematical models and simulation methods. The majority of results confirmed that niche construction can significantly alter the evolutionary trajectories of structured populations. Organism–environmental interactions induced by niche construction can have profound influence on the dynamics, competition and diversity of metapopulations. It can affect fine-scale spatially distribution of species and spatial heterogeneity of the environment. We further propose a few research directions with potentials, such as applying adaptive dynamics or spatial game theory to explore the effect of niche construction on phenotypic evolution and diversification.

Keywords organism-environmental feedback; environmental heterogeneity; individual-based model; diversity.

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1 Introduction

The basic premise of niche construction theory (NCT) is that organism can be described as potent agents of natural selection by modifying their biotic or abiotic environments (Odling-Smee et al., 2013; Matthews et al., 2014). Researches on niche construction have extensively shown how living organisms can alter their surrounding environment through their metabolism, activities, and choices, and by doing so influence their own or others selection pressure (e.g. Jones et al.,1994, 1997; Odling-Smee, et al., 2003; Beerling, 2005; Donohue et al., 2005; Flack et al., 2006; Hoover and Robinson, 2007; Hoover et al., 2011). The new concept proposed in NCT is *ecological inheritance*, which refers to a process of organism-induced environmental modification that can persist for future generations. By doing so, organisms can generate feedbacks with their environment that could potentially alter their evolutionary trajectories (Odling-Smee et al., 2013). This organism-environment feedback is a key factor to decide the spatial structure of species and the system dynamics of communities. To date, NCT has captured the attention from a wide range of evolutionary biologists and ecologists. Matthews et al. (2014) surveyed a large amount of literatures that related to the multiple facets of niche construction, including the NCT itself, a series of studies on evolutionary (e.g. coevolution and speciation) and ecological interactions (especially how ecosystem engineering affects species distribution and turnover). There is, however, a lack of review on the mathematical models for studying the effect of niche construction.

The two-locus population genetic model by Laland is the first theoretical model for exploring the evolutionary consequences of niche construction (Laland et al., 1996, 1999). The analysis confirms that niche construction can be a potent evolutionary agent by generating selection that leads to the fixation of otherwise deleterious alleles, supporting stable polymorphisms, eliminating stable polymorphisms, and generating unusual evolutionary dynamics (Laland et al., 1999).Based on the two-locus population genetic model, some extensive researches were developed. Silver and Di Paolo (2006) presented an individual-based model (IBM) of an extension to the two-locus population genetic model and revealed the importance of spatiality. Niche-construction traits can drive themselves to fixation by simultaneously generating selection that favors ‘recipient’ trait alleles and linkage disequilibrium between niche-construction and recipient trait alleles. Spatial clustering effects is considered a possible mechanism, by which a niche-constructing are trait could establish in an otherwise hostile environment (Silver and Di Paolo, 2006), coincided with the work by Han et al. (2006) who have also incorporated spatial structure into the two-locus genetic model. Taylor (2007) also used an individual-based model to demonstrate that the process of niche construction can indeed introduce an active drive for organisms to possess more genes. This is the first explicit example of a model which demonstrating an intrinsic drive for the evolution of complexity.

Although niche construction has emerged as a central driver of a variety of phenomena that operate over evolutionary time scales, its importance over ecological time scales cannot be denied. Nonetheless, there is insufficient attention to the development of ecological models in enriching the theory of niche construction (Vandermeer, 2004). The flourish of NCT is constrained not only by the progress in its lacking of ecological models, but also by a more intensive exploration of the kind of effects and patterns it can generate. Using the concepts of sufficient viable populations, Vandermeer (2008) developed a framework of differential-equation-based dynamic systems consisting of organisms and their environments and identified that there was a balance between the need for a certain population to maintain the altered/constructed niche and the size of the population that can be sustained by such niche.

The process of niche construction can be evolutionarily and ecologically important to its agents (Kylafis and Loreau, 2008, 2011). In a simple ecosystem of plant-soil nutrient feedbacks, where plants have the ability to increase the input of inorganic nutrient through positive niche construction, plants can foster their own persistence at an ecological time scale; on an evolutionary time scale, niche construction can affect the evolutionary dynamics of the plant and the adaptive regulation of local soil nutrient pool (Kylafis and Loreau, 2008). Moreover, plant’s ability for niche proliferating could interact with its ability for niche deteriorating in modifying the response to environment pressure (Kylafis and Loreau, 2011). In a model of two consumers that compete for one limiting resource but consumed by one predator, niche construction can either generate net interspecific facilitation or strengthen interspecific competition by altering the balance between intraspecific and interspecific competitive effects (Kylafis and Loreau, 2011).

In view of the NCT, organisms are both the object and subject of evolution while adapting to their own environment. The eco-evolutionary feedback that organisms induced during niche construction appears to be an intrinsic property for altruism. Van Dykenand Wade (2012) used the idea of niche construction and constructed a two-trait, co-evolutionary model for social evolution in a structured population and analyzed the long-term phenotypic evolution of the altruistic strategy and their evolutionarily stable strategy (ESS). This model can be further applied to discuss the origins and evolution of eusociality, division of labor, and the interaction between technology and demography in human evolution.

Besides above research progress on theoretical models concerning niche construction, we have also contributed to the field by a set of works. In next section, we summarize our works on how niche construction influences genetic structure of spatially structured populations and the spatio-temporal dynamics of metapopulations affected by niche construction, especially focusing on the aspects of mathematical models and simulation methods. The majority of these theoretical models confirm that niche construction can significantly alter evolutionary trajectories (Hui and Yue, 2005; Han et al., 2006; Han et al., 2009; Han and Hui, 2014), and the organism–environmental relationships induced by niche construction can profoundly influence the dynamics, competition, and diversity of metapopulations (Hui et al., 2004; Yue et al., 2004). In the last section, we propose some thoughts on potential further research, such as applying adaptive dynamics and spatial game theory for studying phenotypic evolution and speciation.

2 Models and Results

The main shortage of two-locus population genetic model is that it neglects the population structure in real-world systems, especially the spatial dimension. Since the spatial structure of populations can influence not only the population dynamics but also the genetic dynamics (e.g. Hanski, 1999; Kritzer and Davies, 2005), we extended the two-locus model onto spatially structured populations and metapopulations.

2.1 Niche construction in spatially structured population

First, we implement a simulation method of a spatially-explicit individual-based cellular automaton (CA) on 200×200 lattices to examine the spatial distribution of genotypes in structured populations, especially along an environmental gradient. The core part of the model is that niche construction of organisms changes the local fitness of all organisms and thereby selects an optimal offspring to keep its genotype. Because different genotypes have different fitness values, the model can be used to study the function of niche construction in polymorphism maintenance (Han et al., 2006). Detailed program is described as follows (see also Han and Hui, 2014).

Let us denote each grid position by$(i,j)$with Neumann neighborhood, containing an isolated population with randomly mating and diploid individuals, and let ***E*** (with alleles *E* and *e*) and ***A*** (with alleles *A* and *a*) be two gene loci of interest. We assume that the frequency of allele *E* at generation *t* affects the individual's capacity of niche construction, and the niche construction can affect the within-cell environmental resource positively or negatively by either producing or consuming the resource. Specifically, in each generation, the amount of resource (*R*) in a specific cell is governed by three processes (independent depletion, renewal and niche construction):

$$R_t(i,j) = \lambda_1 R_{t-1}(i,j)(1-\gamma P_{Et}(i,j)) + \lambda_2 P_{Et}(i,j) + \lambda_3 \quad (1)$$

where $\lambda_1$and λ_3 are coefficients of independent resource depletion and renewal; λ_2 and γ are coefficients of positive and negative niche construction. If there is no niche construction (i.e. $\lambda_2 = 0$ and $\gamma = 0$), the resource will converge to a stable level ($R = \lambda_3/(1-\lambda_1)$). In the following, we ignore negative niche construction (i.e. $\gamma = 0$). Specifically, if the coefficient of independent resource renewal (λ_3) is not a constant but a linear function of the vertical coordinates (*y*), a linear environmental gradientcan be introduced along the *y*-direction.

Generally, we assume $\lambda_3 = ky$, where $k$is an indicator of the gradient of the environmental resource (Han and Hui, 2014). The fitness of organismsof various genotypes is given as below (Table 1; Laland et al., 1999).

Table 1 Genotypic fitness (from Laland et al., 1999; Note the Copyright).

locus	*EE*	*Ee*	*ee*
AA	$\alpha_1\alpha_2+\varepsilon R$	$\alpha_2+\varepsilon R$	$\beta_1\alpha_2+\varepsilon R$
Aa	$\alpha_1+\varepsilon\sqrt{R(1-R)}$	$1+\varepsilon\sqrt{R(1-R)}$	$\beta_1+\varepsilon\sqrt{R(1-R)}$
aa	$\alpha_1\beta_2+\varepsilon(1-R)$	$\beta_2+\varepsilon(1-R)$	$\beta_1\beta_2+\varepsilon(1-R)$

We chose periodic boundaries for the left and right edges to diminish the boundary effect and reflective boundaries for the top and bottom edges. Each cell of the lattices was initially randomly assigned one of the nine genotypes. During each time step, the individual in a focal cell chose to mate with the individual having the highest fitness in four nearest neighboring cells, and then the individual was replaced by its one offspring randomly chosen according to the following fitness-dependent probability P_i:

$$P_i = \frac{\omega_i}{\sum_{i\in\Omega}\omega_i} \quad (2)$$

where Ω is the set of all possible genotypes that the parent can produce;$\omega_i$is the fitness of the i-th genotype. The resource level (R) of this cell was then updated according to Eq. (1).

The simulation of CA model was shown in Fig. 1. When there was no environmental gradient, no clear patterns emerged (Fig. 1a), contrasting to the clear patterns of triple-band (Fig. 1b&c) and double-band distributions of genotypes (Fig. 1d) along the environmental gradient. With the increase of positive niche construction intensity (λ_2), this step-wise form further shifted towards the direction of lower resources and the genotypic distribution was transferred from a double-band to a triple-band pattern. Note that, even without niche construction ($\lambda_2 = 0$), the environmental gradient can still stratify the genotypic distributions. The step-wise form of genotypic diversity suggests that the genotypic diversity reached its peak at an intermediate resource level along the environmental gradient. When further examining the average fitness of the individuals on each row, we found that the fitness landscape along the environmental gradient formed a valley at the intermediate resource level where the transition of genetic composition occurred (Han and Hui, 2014).

2.2 Niche construction in metapopulation

The patch occupant model of metapopulation is a fundamental framework of spatial ecology and is a potent metaphor for population dynamics in patchy environments (Tilman and Kareiva, 1997; Hui and Li, 2003, 2004; Chen and Hui, 2009):

$$\frac{dp}{dt} = cp(1-p) - ep \quad (3)$$

where p is the fraction of patches occupied by the species, c and e are the colonization and extinction rate, respectively. The nontrivial equilibrium $\bar{p} = 1 - e/c$ is globally stable as long as $e < c$. Hui and Yue (2005) used this classical Levins' patch occupant model to probe the effects of niche construction on spatial distribution of metapopulation (see also Hui et al., 2004; Han et al., 2009; Zhang et al., 2012).

Considering a habitat subdivided into discrete patches, each of which can support a local population, assume the metapopulation of diploid individuals and random mating within local populations, defined at one diallelic locus, A, with alleles A (dominant) and a (recessive). Analogous to Laland's assumption (Laland et al., 1999), let us assume that the capacity of niche construction of a local population is influenced by the frequency of genotype aa, F_{aa}. The capacity for niche construction affects the dynamics of a key environmental resource,

$$R_i(t) = \alpha + (1-\beta)R_i(t-1) + \gamma F_{aa}(i, t-1) \qquad (4)$$

where α and $\beta$are coefficients of independent resource renewal and depletion, γ is the coefficient of niche construction.

Furthermore, let us assume that the amount of resource in patch i can influence the fitness of individuals of different genotypes in the patch. Here, we introduce the concept of niche fitness, which is defined as the degree of closeness between the optimum niche point in hyper-volume and the actual resource state. Using the simplest form of resource utilization spectrum (single-humped cure; May, 1981), let the niche fitness of genotype ++ (++ is AA, Aa, or aa) in patch i be defined as:

$$NF_{++}(i,t) = \exp\left(-\delta(R_i(t) - R_{++})^2\right) \qquad (5)$$

where $1/\delta$ is the coefficient of niche breadth, and $R_{++}$is the optimum niche point of genotype ++. We generally adopt this definition of niche fitness to evaluate the influences of niche construction.

In simulations, we utilize Eq. 4 to decide the stochastic dynamics of local extinction and recolonization. At each time step, each local population may go extinct with probability e and the empty patch may be recolonized by its neighboring local populations with probability cn/N(where n and N are the numbers of neighboring populations and neighboring patches, respectively). If there is a local population in patch (i,t)(either from non-extinction or recolonization events), the frequency of genotype ++ (AA, Aa, or aa), $F_{++}(i,t)$, will satisfy the following transition rule:

$$\mathrm{W} \times F_{++}(i,t) = (1-c)F_{++}(i,t-1)NF_{++}(i,t-1) + \frac{c}{N}\sum_{j\in\Omega_i} F_{++}(j,t-1)NF_{++}(j,t-1) \qquad (6)$$

where Ω_i is the set of neighboring serial numbers of patch i, and W is given by the sum of the right-hand sides of Eq. 4 for all the genotypes (Hui and Yue, 2005).

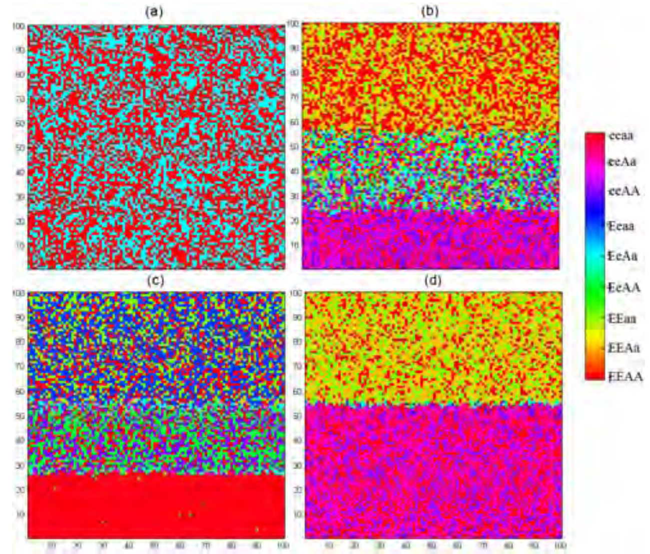

Fig. 1 The distribution of genotypes on environmental gradients under three selection regimes. No environmental gradient in (A), where $\lambda_3 = 0.3$; linear gradient in (B), (C) and (D), with $\lambda_3 = ky$, where $k = 0.003$ along y axis that having 100 coordinated points. Heterozygote superiority is assumed in (A) and (B), with$\alpha_1 = \alpha_2 = 0.99, \beta_1 = \beta_2 = 0.9$; (C) selection only acts on locus A, with $\alpha_1 = \beta_1 = 1, \alpha_2 = 0.8, \beta_2 = 0.9$; (D) selection only acts on locus E, with $\alpha_1 = 0.8, \beta_1 = 0.9$ $\alpha_2 = \beta_2 = 1$. Other parameters are:$\lambda_1 = 0.64, \lambda_2 = 0.05, \varepsilon = 0.3$.

By constructing the one- and two-dimensional spatial lattice models according to the above rules, the evolutionary dynamics and spatial structure of genotype frequencies can be displayed (Fig.2). Due to gene flow and selection, polymorphism can hardly be maintained without niche construction. However, with niche construction polymorphism, even a recessive homozygote can persist in an initially homogeneous patchy habitat. The one-dimensional metapopulation generates a dendritic structure in the temporal-spatial diagram (Fig. 2a–c). Niche construction first filtrates local populations and produces high-degree pure local populations which gradually coalesce and form a distinctive and segregated distribution of pure-line genotype AA and aa. This phenomenon is also obvious in the two-dimensional structures of metapopulations (Fig. 2d–f). The distribution of genotype frequencies forms an archipelago-like spatial structure. The recessive genotype aa forms many islands beset with genotype AA, with hybrids circling these islands. Therefore, niche construction can segregate the distribution of different genotypes and maintain polymorphism in space.

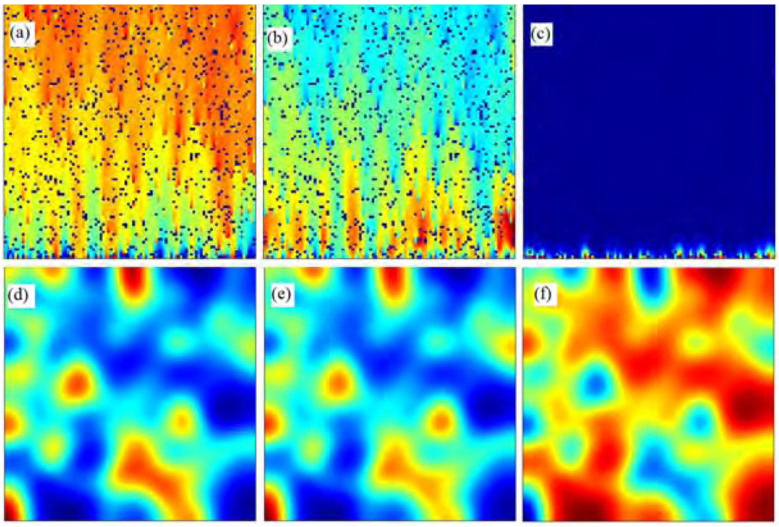

Fig. 2 Dynamics and spatial structures of different genotypes. Different colors in plots represent the frequency of the genotype:(a), (b) and (c) are the evolutionary dynamics and spatial structures of genotypes AA, Aa, and aa , respectively, in a one-dimensional habitat (two nearest neighbors and periodic boundary) with the parameter values: $c = 0.3, e = 0.1, a = 0.05$, $\mathrm{b} = 0.1, \gamma = 0.01,\ \delta = 4,\ \mathrm{R}_{aa} = R_0 + 0.1$. The horizontal axes represent the spatial dimension (100 patches). The vertical axes represent time (200 generations). (d), (e) and (f) are the spatial structures of genotypes AA, Aa, and aa , respectively, in a two-dimensional habitat (100×100patches, four nearest neighbors and periodic boundary) at 200 generations with the parameter values: $c = 0.4, e = 0, a = 0.05,\ \mathrm{b} = 0.1, \gamma = 0.01,\ \delta = 5,\ \mathrm{R}_{aa} = R_0 + 0.05$.

2.3 Time-lagged niche construction in metapopulation

Laland et al. (1996) proposed a time-lagged niche construction and analyzed its influences on evolutionary consequences of population. Here, we use cellular automata to examine the effect of time-lagged niche construction on the spatial pattern of metapopulations. Han et al. (2009) has demonstrated that the time-lag, particularly the primacy effect of time-lag, has a profound effect on the dynamics of niche-constructing metapopulations. Accordingly, the primacy effect was focused in the following.

In the framework of patch occupant model (Eq. 4), we set up grid lattices in a heterogeneous landscape ($\mathrm{n} \times \mathrm{n}$ patches) with synchronized updating, von Neumann neighborhood, and periodic boundaries. Let $P_t(i, j)$ indicate the probability that patch $(i, j)$is occupied by a local population at time$t$.Following Laland et al. (1996), if earlier generations have greater impact on the resource than recent generations (i.e. the primacy effect), the dynamics of resource at time $t$can be depicted as below:

$$R_t = \lambda_1 R_{t-1}(1-\gamma P_t) + \lambda_2 \frac{1-\mu}{1-\mu^n}\sum_{i=1}^{n}\mu^{i-1}P_{t-n+i} + \lambda_3 \quad (7)$$

where μ is a constant. Obviously, the dynamics of resources becomes Eq. (1) when n = 1. The resource level decides the niche fitness of populations. We still use the concept of niche fitness above and denoted as:

$$\omega = \omega_{max}\exp\left(-\delta(\mathrm{R}-R_0)^2\right)(8)$$

where ω_{max} is the maximum niche fitness without external noise; δ is same meaning in Eq. 6. Research on metapopulation theories has suggested that reduced fitness will increase the extinction risk of local populations but decrease the colonization rate,sowe assume that the colonization and extinction rates are, respectively, an increasing and a decreasing function of niche fitness; that is $\mathrm{c} = c'\omega$ and $\mathrm{e} = e'/\omega$, where c' and $e'$are constants.

According to above assumptions, the probability of patch, $P_t(i,j)$, will follow the following iteration formula:

$$P_{t+1}(i,j) = P_t(i,j) + \left[c'\omega_t(\mathrm{i,j})\frac{\sum_\Omega P_{\Omega t}(i,j)}{4}\left(1-P_t(i,j)\right) - \frac{e\prime}{\omega_t(\mathrm{i,j})}P_t(i,j)\right](9)$$

where $\sum_\Omega P_{\Omega t}(i,j)$ is the sum of probability values in neighboring set Ω. Using this probability transition model, the distribution patterns of niche-constructing metapopulation can be explicitly revealed.

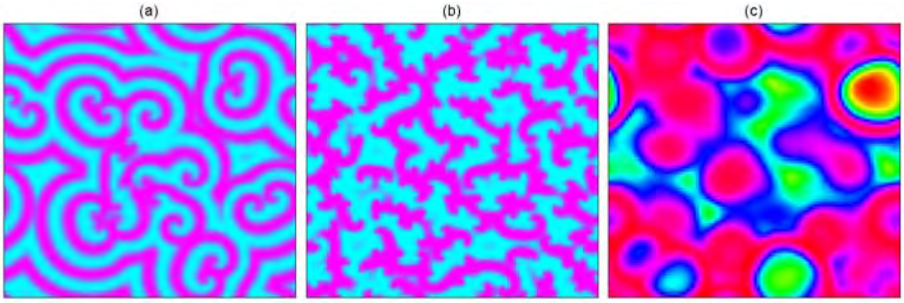

Fig. 3 Three typical spatial patterns of metapopulations: (a) spiral wave, c = 0.6; (b) spiral-broken wave, c = 0.9; (c) circular wave, c = 0.4;Other parameters are:λ_1 = 0.4, λ_2 = 0.6, λ_3 = 0.05.

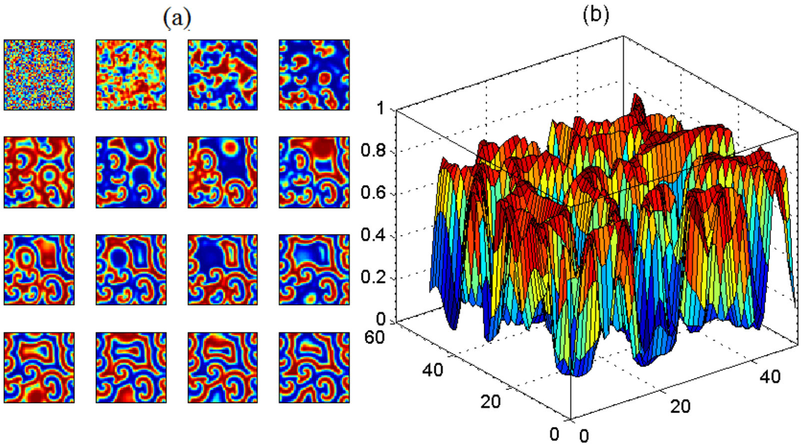

Fig. 4 Snapshots of the dynamics of spatial patterns of the metapopulation (a) and the spatial structure of resource content (b). Parameters are:= 0.6, e = 0.1, λ_1 = 0.4, λ_2 = 0.55, λ_3 = 0.05, γ = 0.1, μ = 0.1, δ = 5.

Three typical spatial patterns emerged in simulation, namely spiral wave (Fig. 3a), spiral-broken wave (Fig. 3b) and circular wave (Fig. 3c). Specially, the spiral waves appeared at moderate colonization rate. When the dispersal capacity of local populations increased to allow accessing the entire habitat, the spiral wave broke into many arms. Moreover, the spatial wave did not travel once stabilized (Fig. 4a). During the initial transition phase (*t*< 500), the spatial structure was changing fast, indicating chaos and turbulence with short-lived spirals. The spiral then gradually formed with many arms, and became stabilized in the habitat. Although the oscillator (due to the time-lag) was still acting on the metapopulation, a fixed spatial structure of the metapopulation was formed. The resource content still exhibited a stable distribution pattern (Fig. 4b). This spatial heterogeneity of environmental resource arose from the niche construction, an ecological imprint of organisms on their environment. It suggests that the environmental heterogeneity and fixed species distribution can be a necessary consequence of this self-organized process of ecological imprint (Han et al., 2009).

2.4 Niche construction in competitive metapopulations

One of the most important results obtained from metapopulation models is the mechanism of competitive coexistence in homogeneous habitat. In this part, we use Tilman's model for simulating the spatial competition of metapopulations (Tilman et al., 1994):

$$\frac{dp_1}{dt} = c_1p_1(1-p_1) - e_1p_1 \qquad (10A)$$

$$\frac{dp_2}{dt} = c_2p_2(1-p_1-p_2) - e_2p_2 - c_1p_1p_2 \qquad (10B)$$

Here p, c and e have the same meaning as in Eq. (4). Species 1 and 2 are the superior and inferior competitors. Tilman's model describes that two competing metapopulation can stably coexist in a spatially implicit homogeneous environment, which requires both an interspecific trade-off in competitive ability versus dispersal ability and a limit to similarity of these traits (Tilman and Kareiva, 1997).

If niche construction can have an impact on interspecific interactions, the dynamics and consequences of competing system will be profoundly affected. Because the superior competitor cannot perceive the inferior one, we only consider the niche construction from inferior species, which can affect the resource content and further determine the fitness of species 1 in patches. Therefore, the dynamics of resource has the following form,

$$\frac{dR}{dt} = \alpha p_2 - \beta R + \gamma \qquad (11)$$

where α is the intensity of niche construction, β and γ are coefficients representing the independent resource depletion and renewal.

Assume that the resource constructed by species 2 can affect the niche fitness of species 1, by which the colonization rate of species 1 is determined. Let the equilibrium of resource content without niche construction,R_0, as the optimum resource content of species 1, hence the colonization rate of species 1 has the following form:

$$\mathrm{c}_1 = c\ \exp\left(-\delta(\mathrm{R}-R_0)^2\right) \qquad (12)$$

Here the various parameters have the same meaning as in Eq. 9. Furthermore, there is always a limited amount of time, energy, and other resources to spend on growth, maintenance and reproduction, so an organism must allocate its resources among these alternative demands (Silvertown and Doust, 1993). For metapopulation, conflicting demands lead to trade-off between abilities of niche construction and colonization. So assume $\mathrm{c}_2 + \mu\alpha = 1$, here μ is a proportional coefficient.

A lattice model with Neumann neighborhood and absorptive boundary was applied to the study of the effect of niche construction on competitive patterns in space (Fig. 5). Through the comparison of spatial patterns with and without niche construction, two results can be obtained. First, the distribution of two species with niche construction was more segregated than the one without niche construction. Resource level in the distribution region of the inferior competitor has been altered by niche construction, which then reduced the colonization rate of the superior competitor into this region and led to the segregation of distributions. Second, the distribution of species with niche construction was more immovable than the one without niche construction. Hence, ecological imprint can segregate and fix the distributions of two species. It implies that we cannot predict species' potential distributions simply according to suitable environmental conditions because such conditions could be a result of niche construction where species' distribution limit can self-emerge through the seemingly cooperative interactions between organisms and their environments (Hui et al., 2004).

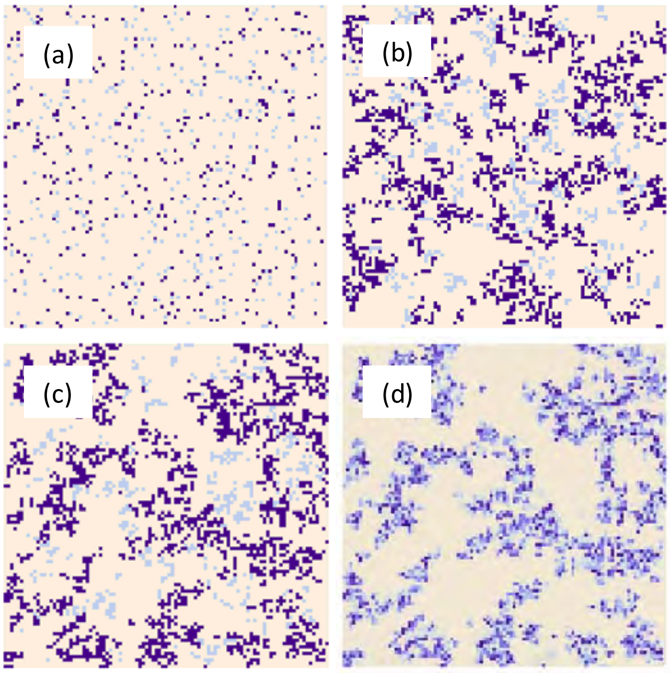

Fig. 5 Distribution of metapopulations with and without niche construction. Blue patches in (a), (b), and (c) depict species 2, and purple patches depict species 1. Blueness in (d) represents the ecological imprint. Lattice model is calculated in two-dimensional space of 100×100patches with 400 randomly located initial local populations for each species. (a) Distribution after 100 generations without niche construction ($\alpha = 0$); (b) distribution after 50 generations from (a) without niche construction ($\alpha = 0$); (c) distribution after 50 generations from (a) with niche construction ($\alpha = 0.2$), and (d) is the spatial distribution of resource content of (c). Parameter values:$\beta = 0.2,\ \gamma = 0.1,\ c = 0.31,\ \delta = 3,\ e_1 = e_2 = 0.2,$ and$c_2 = 0.4$.

3 Discussions

Simulation methods adopted in our works are individual-based models (IBMs),or more specific cellular automata (CAs), which are spatially explicit simulations. Individual-based models (IBMs) are mathematical models in which individual organisms or groups of individuals with the same characteristics are explicitly studied. Over recent years there has been an increasing focus on the use of IBMs and CAs in ecology (Lomnicki, 1998; Hogeweg and Hesper, 1990; McGlade, 1999; Hui and McGeoch, 2006; Roura-Pascual et al., 2009; Hui, 2011; Hui et al., 2011; Ramanantoanina et al., 2011, 2014; Caplat et al., 2014; Donaldson et al., 2014; Su et al., 2008, 2009, 2015). The key motivating force behind the development of IBMs comes from the need to understand the dynamics of spatial systems and the nature of complex behaviors (Bullock, 1994).Wehere showed that the explicit patterns of spatial structure and dynamics, induced by niche construction, can be intriguing and important for polymorphism and diversity maintenance.

Studies on niche construction, particularly using theoretical models, are recently growing in numbers. Besides those have been mentioned in the Introduction section, many others also focus on questions in anthropology, sociology and animal behavior. We here concentrated on the ecological and evolutionary consequences of niche construction, with most involving single or multiple species in the systems (Han et al., 2004; Yue et al., 2004; Hui et al., 2004, 2005; Hui and Yue, 2005; Han et al., 2009; Han and Hui, 2014).Some conclusions are laid on the concept of niche fitness(Li and Lin, 1997). Within the framework of metapopulations, most results came from developing the organism-environment feedbacks in Tilman's competition model (Tilman et al., 1994), which indicates that niche construction can lead to alternative competitive consequences and facilitate coexistence through the trade-off between competition, colonization and niche construction (Hui et al., 2004). The time-lag of niche construction can form a phase-locked oscillation, which then dictates the spatial structure of metapopulations and the environmental heterogeneity that arising from the ecological imprinting process (Han et al., 2009).

In a metacommunity, niche construction could incur oscillations and push some species towards extinction, suggesting a profound influence of niche construction on community structure and assembly rules (Hui et al., 2004). Furthermore, through the coupling relationship between genotypes and key resources, polymorphism can be maintained in a metapopulation even without heterozygote superiority (Hui and Yue, 2005). This result is in agreement with those for spatially structured populations (Han et al., 2006). In particular along the environmental gradient, niche construction can stratify genetic diversity and promote reproduction isolation by forming a fitness valley, which depends on heterogeneous environments, resource-dependent fitness and the selection force acting on the niche-constructing gene loci (Han and Hui, 2014). The above research suggests that the niche-constructing feedback between an organism and its environment is an active force to change the environments and hence the direction of natural selection.

The new term of 'ecological imprint' has been proposed based on our studies. In metapopulation, lattice models suggest that 'ecological imprint' of organisms on environments is formed by reinforcing niche construction, consequently forming fine-scale spatial heterogeneity of environmental resources (Hui et al., 2004; Han et al., 2009). The distribution of metapopulation is closely matched with this ecological imprint. It leads to the self-organized spatial heterogeneity of environment and species' distribution limits (Han et al., 2009). In competitive systems, ecological imprint can weaken the intensity of spatial competition and segregates species distributions (Hui et al., 2004). Traditionally, spatial heterogeneity arises from geographical and geological interactions. However, our results imply that spatial heterogeneity and species' distribution limit may be, at least at the local scale, the byproducts of ecological imprint. Consequently, niche construction can connect spatial heterogeneity and biotic interactions and may be an important factor leading to the distribution limit of species.

Although there area large number of literatures on niche construction, they mainly involve single- or multi-species, with simple abiotic or biotic interactions. For instance, we only considered niche construction behaviorto contribute to the fitness of particular organisms or genotypes and adopt a Gaussian function of fitness to measure the magnitude of feedback between organisms (and genotypes) and their environments. We may, in the future, make progress by building new modeling systems of eco-evolutionary dynamics (Matthews et al., 2014). This could be done by using the following candidate methods. First, adaptive dynamics is a mathematical approach for studying evolutionary changes when fitness is density or frequency dependent, where ecological interactions can drive evolutionary dynamics of a system (Metz et al., 1992; Doebeli and Dieckmann, 2000). It was frequently used to discuss core problems in evolutionary biology, especial polymorphism and diversification through evolutionary branching (e.g., Zhang et al., 2013; Landi et al., 2015). Adaptive dynamics describes evolution as a process of small successive steps of mutation and invasions of rare mutant traits, using the concept of invasion fitness (Metz et al., 1992). Kylafis and Loreau (2008) have followed this approach to verify that the adaptive response of niche-constructing plants in external environments can result in the emergence of a regulatory process at the evolutionary time scale. The methodology of adaptive dynamics could hold the key for further breakthroughs in studying the function of niche construction on evolution. Another approach can be used for studying the evolutionary consequence of niche construction is the game theory, which is an approach for identifying the best strategy under certain conditions. Each player in the game tends to choose the strategy that can maximize its payoff which is also dependent on the strategies of the co-players (e.g. Hui, 2008; Hui and McGeoch, 2007; Zhang and Hui, 2011). Organisms with various phenotypes for niche construction can be viewed as different players, and they are engaging with each other in a multi-player game to pursuit their own optimal payoffs.

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