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On the interplay of speciation and dispersal: An evolutionary food web model in space

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HIGHLIGHTS

- We analyze the interplay of evolution and dispersal in metacommunities.
- Locally, food webs evolve according to the model by Loeuille and Loreau (2005).
- By coupling these via migration links, we obtain food webs in a patchy environment.
- Random migration leads to familiar diversity–dispersal relationships.
- With adaptive migration, neighboring networks can become very different.

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ABSTRACT

We introduce an evolutionary metacommunity of multitrophic food webs on several habitats coupled by migration. In contrast to previous studies that focus either on evolutionary or on spatial aspects, we include both and investigate the interplay between them. Locally, the species emerge, interact and go extinct according to the rules of the well-known evolutionary food web model proposed by Loeuille and Loreau (2005). Additionally, species are able to migrate between the habitats. With random migration, we are able to reproduce common trends in diversity–dispersal relationships: Regional diversity decreases with increasing migration rates, whereas local diversity can increase in case of a low level of dispersal. Moreover, we find that the total biomasses in the different patches become similar even when species composition remains different. With adaptive migration, we observe species compositions that differ considerably between patches and contain species that are descendant from ancestors on both patches. This result indicates that the combination of spatial aspects and evolutionary processes affects the structure of food webs in different ways than each of them alone.

1. Introduction

Classical food web models represent an idealization of real ecosystems that focuses on feeding relationships as the most important type of interaction and that considers populations as well mixed and homogeneous in space. Typically, such models include nonlinear differential equations that capture the growth and loss terms of population dynamics, and a simple stochastic algorithm for generating network structures with realistic features, such as the niche model (Williams and Martinez, 2000) or the cascade model (Cohen and Newman, 1985; Cohen et al., 1980). They provide a static, mean field description, integrating the feeding relationships across the whole spatial extent of the system and ignoring temporal changes in the composition of the network due to species turnover.

In order to go beyond mean-field models, various approaches have been taken to include spatial structure or species turnover in food web models. If space has the structure of discrete habitats, one obtains "networks of networks". The outer network represents the spatial landscapes consisting of several habitats, the connections between them representing possible routes for dispersal. A chain topology of habitats results for instance for a river with barrages, and a ring of habitats can occur along island shores. More complex spatial networks might represent archipelagos, or a system of waterbodies connected by streams and canals. The inner networks describe localized food webs on these habitats, the connections between species representing feeding relationships. The need to study such spatially extended food webs has been highlighted recently by several authors (Hagen et al., 2012; Gonzalez et al., 2011; Amarasekare, 2008; Leibold et al., 2004). Most studies of spatial ecosystems concentrate on simple topologies of the inner

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network, such as food chains (Calcagno et al., 2011) or small food web motifs of two (Jansen, 2001; de Roos et al., 1998), three (Reichenbach et al., 2007; Koelle and Vandermeer, 2005; Holt, 2002; Blasius et al., 1999) or four (Ristl et al., 2014) species in space. So far, there exist few investigations of larger food webs in space, both empirical (Legrand et al., 2012; Logue et al., 2011; Presley and Willig, 2010; Cottenie et al., 2003), and theoretical (Haegeman and Loreau, 2014; McCann et al., 2005; Mouquet and Loreau, 2002, 2003; Wilson, 1992). Moreover, all of the mentioned studies focus on spatial aspects under the assumption that the species composition is static.

On the other hand, studies addressing species turnover typically neglect spatial aspects. During the last years, several models were introduced that include evolutionary dynamics (for references see next paragraph). On a time scale much slower than population dynamics, new species, which are modifications of existing species, are added to the system. They can be interpreted either as invaders from another, not explicitly considered spatial region, or as arising from a speciation process. Population dynamics then determines which species are viable. In contrast to static models such as the niche model, the food web structure is not put in by hand, but emerges from the interplay between population dynamics and species addition. Evolutionary food web models can therefore give insights into the conditions under which complex network structures can emerge and persist in face of ongoing species turnover. They are thus fundamentally different from species assembly models, which have been studied for a longer time and which are based on a fixed species pool from which species are added to a smaller habitat.

Loeuille and Loreau (2005) introduced the probably simplest successful evolutionary food web model. In contrast to other well-known evolutionary food web models, like for example the matching model (Rossberg et al., 2006, 2008) or the webworld model (Caldarelli et al., 1998; Drossel et al., 2001, 2004), which describe a species by a vector of many abstract traits, a species in this model is specified only by its body mass. The feeding relationships are determined by differences in body mass. A version with gradual evolution was studied by Brännström et al. (2011). Ingram et al. (2009) extended the model to include an evolving feeding range, and Allhoff and Drossel (2013) also considered a version with an evolving feeding center. These extensions make the model very similar to the evolving niche model (Guill and Drossel, 2008), where the niche value can be equated with the logarithm of the body mass, and where also these three parameters are evolved. In contrast to the simpler model by Loeuille and Loreau (2005), these models need additional ingredients that prevent evolution from running to extremes, such as adaptive foraging or restrictions on the possible trait values (Allhoff and Drossel, 2013).

Recently, several authors emphasized that combining the spatial and the evolutionary perspective on ecosystems is essential for better understanding coexistence and diversity (Logue et al., 2011; Urban and Skelly, 2006; Urban, 2006; Urban et al., 2008). It is well known that including a spatial dimension in evolutionary models enables the coexistence of species or strategies that would otherwise exclude each other (Szabó and Fáth, 2007). This is due to the formation of dynamical waves in which the competitors cyclically replace each other, or to the formation of local clusters that cannot easily be invaded from outside. However, these studies are usually limited to two or three species. A recent study of a larger system was published in 2008 by Loeuille and Leibold (2008a), who investigated a metacommunity food web model with two plant and two consumer species on a patchy environment, where one of the plant species has evolving defense strategies. The authors demonstrated the emergence of morphs that could only exist in a metacommunity due to the presence of dispersal highlighting the fact that the combination of space and evolutionary processes yields important new insights.

In this paper, we study the combined effect of space and evolution on food webs consisting of many species on up to four trophic levels. We use the model of Loeuille and Loreau (2005), placing it on several habitats that might represent lakes, islands or a fragmented landscape, and that are coupled by migration. The results are “evolutionary networks of networks”. By varying migration rules (undirected, directed, diffusive, adaptive, dependent on body mass), the time of migration onset (at the beginning or after local food webs have evolved), and the number and properties of habitats (2 or 8 habitats, equivalent or differing with respect to simulation parameters), we investigate many different scenarios.

With diffusive migration, our results agree qualitatively with diversity–dispersal relationships from empirical studies (Sax and Gaines, 2003) and from other theoretical metacommunity studies (Mouquet and Loreau, 2002, 2003; Urban, 2006). Low migration rates lead to an increased diversity in the local habitats, and high migration rates lead to homogenization of habitats and hence to a decreased regional diversity. For a chain of eight habitats coupled by diffusive migration, we find that migration leads to equal biomasses in the habitats, even when the species composition of neighboring patches is very different. With adaptive migration we obtain networks that differ strongly in their species composition but that do not show increased local diversity.

2. Model and methods

2.1. The model by Loeuille and Loreau on one habitat

The model by Loeuille and Loreau (2005) includes population dynamics on the one hand and the introduction of new species via modification of existing species on the other. Because such “mutation” events are very rare, population dynamics typically reaches an attractor before the introduction of a new species. Thus, ecological and evolutionary time scales can be viewed as separate.

Population dynamics is based on the body mass x_i of a species $i \in \{1, \dots, n\}$ as its only key trait. Species are sorted such that body mass increases with index number. Production efficiency f and mortality rate m scale with body masses according to the allometric relations $f(x_i) = f_0 x_i^{-0.25}$ and $m(x_i) = m_0 x_i^{-0.25}$. The population dynamics of species i with biomass N_i is given by

$$
\begin{aligned}
\frac{dN_i}{dt} = {} & f(x_i) \sum_{j=0}^{i-1} \gamma_{ij} N_i N_j \quad \text{(predation input)} \\
& - m(x_i) N_i \quad \text{(mortality)} \\
& - \sum_{j=1}^{n} \alpha_{ij} N_i N_j \quad \text{(competition)} \\
& - \sum_{j=i+1}^{n} \gamma_{ji} N_i N_j \quad \text{(predation loss)}
\end{aligned}
\tag{1}
$$

with

$$
\gamma_{ij} = \gamma(x_i - x_j) = \frac{\gamma_0}{s\sqrt{2\pi}} \exp\left(\frac{-(x_i - x_j - d)^2}{s^2} \right) \tag{2}
$$

describing the rate with which predator i consumes prey j, and with

$$
\alpha_{ij} = \begin{cases} \alpha_0 & \text{if } |x_i - x_j| \le \beta \\ 0 & \text{else} \end{cases} \tag{3}
$$

describing the competition strength. The parameters γ_0, d, s, and β are the integrated feeding rate, the preferred body mass difference between predator and prey, the width of the feeding niche, and the competition range.

Energy input into the system is provided by an external resource of “body mass” $x_0 = 0$ and total biomass N_0, which is