Impact of stochastic migration on species diversity in meta-food webs consisting of several patches

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ABSTRACT

The structure of space has an appreciable influence on the diversity and stability of ecosystems. So far, there are only few theoretical studies investigating the population dynamics of food webs consisting of many species that can migrate between several patches, and in most of these models migration is a continuous, deterministic process. However, when migration events are rare (for instance because the patches are far apart), migration is a stochastic process and should be modeled accordingly. We present computer simulations of a food web model of many species on a spatial network of several patches, combining deterministic local population dynamics with stochastic migration. We evaluate the influence of the migration rate and other model parameters on local and regional species diversity and on stability. We find that migration increases the number of surviving and coexisting populations by two effects. These are the rescue effect, which restores local populations that have gone extinct, and dynamical coexistence, which sustains local populations that could not persist in the absence of immigration. Both effects occur even when migration events are rare. Species diversity increases on local and regional scales with the frequency of migration events. Furthermore, we investigate the adiabatic limit in which population dynamics always reaches an equilibrium before the next migration event, and we investigate the possible long-term scenarios. While the final state often contains the same food web on all patches, we also find instances where two slightly different food webs coexist on different patches, even when initially each patch contained the same food web.

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1. Introduction

One of the most important goals of the theoretical investigation of food webs is the identification of factors that enhance their stability and diversity (May, 1972; 1973; McCann, 2000). Many studies so far focussed on spatially fully mixed models, identifying stabilizing factors such as empirically consistent food web topologies (Martinez et al., 2006; Yodzis, 1981) and interaction strength distributions (Gross et al., 2009; McCann et al., 1998), allometric scaling (Brose et al., 2006; Kartascheff et al., 2010; Yodzis and Innes, 1992), and adaptive foraging (Heckmann et al., 2012; Kondoh, 2006; Uchida et al., 2007). In several classical studies, stability is evaluated as the probability that a fixed point of the dynamics is stable (Gross et al., 2009; May, 1972). However, species can persist even when their dynamics does not approach a fixed point (Brose et al., 2006). Therefore, the percentage of species that persist in a food web, also called (community) robustness (Brose et al., 2003; Heckmann et al., 2012; Kartascheff et al., 2010; Plitzko and Drossel, 2015) or population persistence (Brose et al., 2006), is

used as a stability criterion. Since this robustness is evaluated by starting with random, i.e., nonequilibrium population sizes, it bears some resemblance to the more general concept of robustness as the persistence of features in a system's response to perturbations (Pascual and Dunne, 2006).

In addition to local factors, spatial structure has a strong effect on the survival and diversity of species. This leads to the investigation of metacommunity models (Levins, 1969) which consist of several local patches, each containing several species (Holyoak et al., 2005). Dispersal between patches enhances species survival and coexistence (Dey and Joshi, 2006; Hauzy et al., 2010; Holyoak and Lawler, 1996; Molofsky and Ferdy, 2005; Plitzko and Drossel, 2015), since species can be rescued from extinction by immigration from neighboring patches, and since the increased size of the phase space allows for new dynamical attractors. Intermediate migration rates have the strongest stabilizing effect, as high migration rates lead to synchronization of the population dynamics on the different patches, which in turn increases the global extinction risk because all populations have their minimum at the same time. Until now, the impact of migration on species survival and coexistence has been studied mostly in simple systems

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like predator-prey communities (Hauzy et al., 2010; Holyoak and Lawler, 1996) or metapopulations (Dey and Joshi, 2006; Molofsky and Ferdy, 2005). Plitzko and Drossel (2015) extended previous studies to complex metacommunities with several trophic levels consisting of up to 60 species on 20 patches.

The investigations mentioned so far use deterministic equations to describe population dynamics within each patch and migration between patches. Such an idealization is necessary in order to calculate many populations within a short computation time, and it is appropriate when populations are large and migration events are frequent (Allen, 2010; Kurtz, 1970). However, when these conditions are not fulfilled, stochastic effects become important. Stochastic effects can considerably change the behavior of a system compared to its deterministic version and lead to extinctions, to shifts of equilibria and of bifurcations, or to periodic oscillations (Black and McKane, 2012; Grima, 2010; McKane and Newman, 2005). Several empirical studies ascribe their findings to stochastic effects (Antonovics and Edwards, 2011; Higgins et al., 1997; Krkošek et al., 2011).

Accordingly, stochasticity was integrated in ecological models in many different ways. Several studies investigated local and regional persistence under the influence of environmental fluctuations (Lande, 1993), resource fluctuations (Bulte and van Kooten, 1999), fluctuation of interactions (Keeling and Gilligan, 2000), and random fluctuations in the local birth and death rates (Lande, 1993), also known as demographic stochasticity (Yaari et al., 2012). Such fluctuations can increase the risk of extinction, but they can also further coexistence.

An often chosen approach for stochastic dynamics is individual-based modeling, with time evolution being a stochastic process based on reaction and transition rates (Alonso and McKane, 2002; Black and McKane, 2012; Economo and Keitt, 2008; 2010; Hubbell, 2001; McKane and Newman, 2004; Ross, 2006; Ross et al., 2008; Yaari et al., 2012). However, individual-based modeling is computationally very expensive and is usually not used for studies of larger ecological and spatial networks, with neutral models being an important exception (Economo and Keitt, 2008; 2010; Hubbell, 2001; Warren, 2010). Therefore, stochastic models on a metacommunity level often focus on the birth-death dynamics of entire populations and uses effective dynamical rules for colonization and extinction processes (Alonso and McKane, 2002; Black and McKane, 2012; Ross, 2006; Ross et al., 2008), calculating for instance life time distributions (Alonso and McKane, 2002), optimal strategies in the presence of trade-offs between good dispersal ability and good competitive ability (Ross et al., 2008), or the decrease of α-diversity along a chain of islands (Warren, 2010).

In recent years, stochastic metapopulation models with explicit population dynamics were created by adding noise terms to the deterministic differential equations or by making stochastic transitions between discrete values of the population size (Simonis, 2012; Yaari et al., 2012). Such models were used to investigate the effect of dispersal on species survival and synchronization, finding that stochasticity reduces the synchronizing effect of dispersal in predator-prey metapopulations (Simonis, 2012) and that higher dispersal rates lead to longer persistence times (Yaari et al., 2012). However, these studies focus on simple systems of one or two species only.

Economo and Keitt (2008, 2010) used the neutral model on a metacommunity level and investigated the influence of increasing migration rates on α-, β-, and γ-diversity. Similar to what was found with deterministic models, they found that α-diversity increases for all nodes at the expense of β-diversity.

So far, there exists no study that explores the effect of stochasticity on species survival and diversity in meta-food webs that contain several trophic layers and thus take into account the fact that species survival depends strongly on trophic interactions. The above-mentioned deterministic models (Plitzko and Drossel, 2015) become very unrealistic when migration rates are small, because in this limit deterministic modeling results in a continuous and very small flow of biomass between patches, while in reality low migration rates mean that an integer number of individuals moves occasionally from one patch to another. Obviously, even very rare migration events can reestablish populations on patches where they went extinct; but this is not observed with a deterministic modeling approach, where the very small biomass influx cannot establish a population size above the extinction threshold (Plitzko and Drossel, 2015). Since dispersal rates are often orders of magnitude lower than birth or mortality rates (Hanski, 1998), this limit of low migration rates is empirically very relevant.

In this paper, we want to fill this gap and use a meta-food web model with stochastic migration in order to investigate the effect of dispersal on species persistence and diversity. Just as in the study by Plitzko and Drossel (2015), we use the niche model with the bioenergetics approach developed by Yodzis and Innes (1992). We use deterministic population dynamics within patches and model only migration as a stochastic process. By comparing to the fully deterministic case, we can thus distill the effect of stochastic migration alone. We use community robustness as stability criterion and analyze how the frequency of migration events impacts robustness on local and regional scales. We focus on the role of the different trophic levels and discuss in particular the adiabatic limit of very rare migration events. In this limit we find that stochastic migration increases robustness compared to the deterministic case, and that after a long time either all patches host the same food web or a small number of slightly different food webs.

2. The model

Our model consists of several patches (usually four), each containing a local food web. On each patch, population dynamics is described by differential equations that take the trophic interactions into account. Between patches stochastic migration events occur. Starting with random initial population sizes, local and spatial dynamics are evaluated until an attractor is reached. We then evaluate the proportion of persisting species (i.e., the community robustness Brose et al., 2003) and average over many runs. In more detail, the model is as follows:

2.1. Local food web

The local food webs were constructed using the niche model (Williams and Martinez, 2000). First, the number of species S and the average connectance C was chosen. To each species, a random niche value $n_i \in [0, 1]$, a random feeding center $c_i \in [n_i r_i/2, n_i]$, and a feeding range $[c_i - n_i r_i/2, c_i + n_i r_i/2]$ were assigned. The value of $r_i \in [0, 1]$ was drawn from a beta-distribution $P(r|1, b) = b(1 - r)^{b-1}$, with $b = (1 - 2C)/2C$ (Williams and Martinez, 2000). All species i with a niche value in the feeding range of species j, were assigned as a prey to species j. Note that we excluded cannibalism. All species without prey were interpreted as basal species which obtain their energy from a constant external resource pool.

In order to make sure that different food webs have similar energy flows, we only used food webs with an actual connectance that differed by less than 0.1 from the average connectance $C = 0.15$ put into the niche model, and a number of basal species $B_{\text{input}} = S/6$, rounded to the next integer (Kondoh, 2006), with S being the number of species.

We defined the trophic level of a species to be the number of links that give the shortest path to the resource.