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## The influence of dispersal on a predator–prey system with two habitats

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## H I G H L I G H T S

- We investigate a predator–prey system on two coupled patches.
- We evaluate stability and bifurcations for many model classes.
- Losses due to emigration and adaptive dispersal can be stabilizing.
- Dispersal can induce pattern-forming bifurcations.
- Adaptive dispersal leads to antisynchronous oscillations.

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## A B S T R A C T

Dispersal between different habitats influences the dynamics and stability of populations considerably. Furthermore, these effects depend on the local interactions of a population with other species. Here, we perform a general and comprehensive study of the simplest possible system that includes dispersal and local interactions, namely a 2-patch 2-species system. We evaluate the impact of dispersal on stability and on the occurrence of bifurcations, including pattern forming bifurcations that lead to spatial heterogeneity, in 19 different classes of models with the help of the generalized modelling approach. We find that dispersal often destabilizes equilibria, but it can stabilize them if it increases population losses. If dispersal is nonrandom, i.e. if emigration or immigration rates depend on population densities, the correlation of stability with dispersal rates is positive in part of the models. We also find that many systems show all four types of bifurcations and that antisynchronous oscillations occur mostly with nonrandom dispersal.

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## 1. Introduction

In ecology both the exploration of dynamical models of food webs (Pascual and Dunne, 2005; Thompson et al., 2012; Rooney and McCann, 2012) and the study of spatial metapopulations (Holland and Hastings, 2008; Hanski and Gaggiotti, 2004; Tromeur et al., 2013) are well established lines of research. The two modelling approaches emphasize different aspects of ecological dynamics that are both relevant for most species: the dispersal between different habitat patches and trophic interactions with other species. Yet, models that combine dispersal with trophic dynamics have only recently begun to appear. In the following we refer to such models that include both these features as meta-foodwebs.

An elegant meta-foodweb model that is based on rates for colonization and extinction was proposed by (Pillai et al., 2011). More detailed dynamical models were proposed in Abrams and Ruokolainen (2011), Abdillaoui et al. (2007), and Jansen (2001), to name a few. The different models draw motivation from different biological systems and hence make different modelling choices regarding the nature of dispersal and local dynamics. For example Jansen (2001) assumes diffusive dispersal between patches which is appropriate for simple life forms such as bacteria, whereas Abrams and Ruokolainen (2011) make dispersal dependent on growth rate differences between patches, implying that individuals can actively choose the site with the best growth conditions. Though many of these studies only describe two patches, conclusions from multi-patch models are often consistent with those from two-patch models (Jansen and de Roos, 2000), and therefore the insights gained from 2-patch systems have wider applications.

The two mentioned examples for implementing dispersal are only a small subset of the large space of possibilities. In the literature different assumptions are made regarding the functional

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forms of the number of emigrants from a given habitat patch, the choice of destination, the proportion of survivors that arrive as immigrants in the destination patch and the settlement success (Amarasekare, 2008; Armsworth and Roughgarden, 2008; Rowell, 2010). In the simplest case a fixed proportion of the population emigrates per unit time and instantaneously and losslessly settles in a randomly chosen neighbouring patch (Leibold et al., 2004). This type of migration is usually called “random dispersal” or “diffusive migration”, and often leads to a synchronisation of the population dynamics of the two patches (Goldwyn and Hastings, 2008; Jansen, 2001). Examples for non-random dispersal are predator evasion and predator pursuit (Li et al., 2005), or a migration rate that is proportional to the difference in growth rates between two patches (Abrams and Ruokolainen, 2011).

The type of dispersal strongly affects the stability and the dynamics of the system. In general, more rapid dispersal is more likely to synchronize populations, although synchronisation does not necessarily require strong dispersal (Liebhold et al., 2004). With adaptive dispersal, antisynchronous oscillations of the two patches are observed, which increase metapopulation persistence. The less similar populations are the less likely is it that dispersal is synchronizing (Esa Ranta and Lundberg, 1998). Other authors find that increased dispersal can decrease synchrony in population dynamics depending on the interactions between migrating species (Koelle and Vandermeer, 2005). A general investigation of metapopulations based on a linear stability analysis (Tromeur et al., 2013) found that costly dispersal and social fencing are stabilizing, while positive density dependence and settlement facilitation reduce stability. Other papers have shown that costly dispersal might be destabilizing to a metapopulation with homogeneous patches (Kisdi, 2010) so the specific mechanisms appear to be of importance. The effects of dispersal on stability can depend not only on the type but also on the intensity of the dispersal (Briggs and Hoopes, 2004).

While much progress has been made for metapopulations and for specific example systems for meta-foodwebs, a broad and general understanding of how different factors impact the stability of meta-foodwebs is still lacking. For instance is it unclear under which conditions dispersal has a stabilizing impact. Furthermore, meta-foodwebs can potentially undergo various types of instabilities. The study of foodwebs has provided abundant examples of two basic mechanisms of instability. The saddle-node bifurcation, which can lead to the relatively sudden collapse of populations, and the Hopf bifurcation, which gives rise to (at least transient) oscillations. In meta-foodwebs both of these instabilities can occur in two variants. The first of these affects all patches equally and is thus closely related to the bifurcations in non-spatial food web models. In the second type different patches are affected differently. They are thus reminiscent of pattern-forming instabilities such as the Turing and wave-instabilities, which are known from systems of partial differential equations (Segel and Jackson, 1972). While also these bifurcations lead to instability, their impact on the overall population density is less pronounced, and they act as drivers of heterogeneity, which, in the long run, might benefit the system. In addition to these four types of instabilities, meta-foodwebs show further instabilities that occur out of the attractors created by these basic bifurcations, such as bifurcations involving heterogeneous fixed points, and nonlocal bifurcations involving limit cycles or strange attractors.

In order to gain an overview of the possible dynamical patterns of a system and their requirements, the generalized modelling approach (Gross and Feudel, 2006; Yeakel et al., 2011; Gross et al., 2009), which is based on a linear stability analysis of steady states, is particularly powerful. The idea behind this approach is to consider models where the kinetics of some processes have not been restricted to specific functional forms. Considering a model with a

specific structure, but containing general functions, allows capturing well-known insights into the structure of the system, without requiring often questionable assumptions on the exact form of kinetics. Further advantages are a short computation time and ease of biological interpretation. We will confine our study to bifurcations out of homogeneous equilibria. This means that instabilities of heterogeneous systems and nonlocal bifurcations are not considered.

In this paper, we investigate the dynamics of two species on two identical patches using the generalized modelling approach. We are able to analyse a broad class of models that includes several previously studied systems as special cases. We focus on the effect of the type and strength of migration on the stability and the dynamics of the system. We find migration in most cases to be either destabilizing or to have a marginal effect on stability. However, complex migration rules allow for a stabilizing influence of dispersal and can produce saddle-node and Hopf bifurcations and spatial-pattern forming bifurcations.

## 2. Model

### 2.1. Generalized modelling formulation

We consider a system consisting of two habitat patches, where each patch  $i$  can potentially sustain a prey population  $X_i$  and a predator population  $Y_i$ . We assume a homogeneous system, such that both patches are described by identical parameter values. The population dynamics are described by

$$\begin{aligned}\dot{X}_1 &= G(X_1) - K(X_1) - F(X_1, Y_1) + \eta^X E^X(X_2, Y_2, X_1, Y_1) - E^X(X_1, Y_1, X_2, Y_2) \\ \dot{Y}_2 &= \lambda F(X_1, Y_1) - D(Y_1) + \eta^Y E^Y(X_2, Y_2, X_1, Y_1) - E^Y(X_1, Y_1, X_2, Y_2) \\ \dot{X}_2 &= G(X_2) - K(X_2) - F(X_2, Y_2) + \eta^X E^X(X_1, Y_1, X_2, Y_2) - E^X(X_2, Y_2, X_1, Y_1) \\ \dot{Y}_2 &= \lambda F(X_2, Y_2) - D(Y_2) + \eta^Y E^Y(X_1, Y_1, X_2, Y_2) - E^Y(X_2, Y_2, X_1, Y_1),\end{aligned}\quad (1)$$

where we used the dot over a variable to indicate the temporal derivative. The variables are in arbitrary units. For the purpose of this paper we will assume that they describe the system in terms of carbon biomass density, however, the same equations also apply to other measures of population, such as abundance. The prey population density changes due to a growth rate  $G(X_i)$ , a respiration/mortality rate  $K(X_i)$ , and a rate of biomass loss by predation  $F(X_i, Y_i)$ . Predator populations have a growth term  $\lambda F(X_i, Y_i)$ , with the prefactor  $\lambda$  describing the efficiency of the energy conversion. The respiration/mortality rate of the predator is given by  $D(Y_i)$ . The rate of emigration is  $E^U(\mathbf{X}, \mathbf{Y})$  for both species  $U = X, Y$  and the migration loss factor is  $\eta^U$ . In the most general case, emigration rates depend on all four populations. The case where the emigration rate of population  $U_i$  is proportional to  $E_i$  and independent of other variables corresponds to diffusive migration, otherwise we get different versions of adaptive migration.

Modes of the form Eqs. (1) can have multiple feasible steady states, depending on the choice of functional forms and parameter values. In the generalized model we cannot compute the steady states. However, a central insight is that we can still compute conditions for the stability of steady states and express them in the form of meaningful ecological parameters. For this purpose we consider an arbitrary feasible, but not necessarily stable steady state.

The normalized biomasses are

$$x_i = \frac{X_i}{X_i^*}, \quad y_i = \frac{Y_i}{Y_i^*} \quad (2)$$

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