



Impact of dispersal on the stability of metapopulations



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HIGHLIGHTS

- We propose a metapopulation model that captures the spatial dynamics of a species.
- We explore the model without restricting the kinetics to specific functional forms.
- The results offer a broad perspective on the dynamical stability of metapopulations.
- Density-dependent dispersal and settlement are shown to influence stability.
- Network topology is shown to affect the impact of dispersal on stability.

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ABSTRACT

Dispersal is a key ecological process that enables local populations to form spatially extended systems called metapopulations. In the present study, we investigate how dispersal affects the linear stability of a general single-species metapopulation model. We discuss both the influence of local within-patch dynamics and the effects of various dispersal behaviours on stability. We find that positive density-dependent dispersal and positive density-dependent settlement are destabilizing dispersal behaviours while negative density-dependent dispersal and negative density-dependent settlement are stabilizing. It is also shown that dispersal has a stabilizing impact on heterogeneous metapopulations that correlates positively with the number of patches and the connectance of metapopulation networks.

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1. Introduction

Many species occupy disconnected habitats that consist of individual patches linked by dispersal (MacArthur and Wilson, 1967). Understanding the dynamics of such species requires describing them as a meta-population that is formed of populations in the respective patches (Levins, 1969; Hanski, 1999). Untangling the influence of dispersal on the stability of such metapopulations is a major challenge.

While the investigation of metapopulation dynamics classically relies on extinction-colonization models (Hanski, 1998), recent progress has been made by extending population-dynamical models to the metapopulation context. Dispersal in metapopulations has been found to be both stabilizing and destabilizing, depending on the intensity of dispersal (Briggs and Hoopes, 2004). It is generally thought that weak dispersal stabilizes metapopulations by generating asynchronous dynamics between patches (Taylor, 1990; Ruxton, 1994; Briggs and Hoopes, 2004), while

strong dispersal is expected to destabilize metapopulations by promoting greater synchrony between patches (Hastings, 1993; Ruxton, 1994). However, it has been shown that metapopulation synchrony and stability may also be positively correlated (Abbott, 2011). Further, the influence of dispersal on stability is crucially mediated by local dynamics and dispersal behaviours (Amarasekare, 1998, 2004).

Dispersal behaviours are life history traits that affect the fitness of individuals in heterogeneous landscapes (Dieckmann et al., 1999). Although dispersal has long been modelled as a linear, density-independent behaviour (Bascompte and Solé, 1994), it now appears that density-dependent dispersal is a widespread strategy (Bowler and Benton, 2005), that can appear as a result of eco-evolutionary dynamics (Travis et al., 1999). Dispersal-related behaviours take various forms, in all steps of dispersal: emigration, inter-patch movement and immigration (Bowler and Benton, 2005). For instance, emigration can be triggered by an over-crowded patch and immigration can be enhanced or inhibited by a high density of conspecifics. While adaptive, these behaviours may also affect the dynamics of metapopulations and bring local populations on the edge of extinction (Dieckmann et al., 1999).

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Bascompte and Solé (1994) found that increasing density-independent dispersal can destabilize metapopulations, whereas Hassell et al. (1995), followed by Rohani et al. (1996) and Jang and Mitra (2000), concluded that it does not influence stability. Further, it has been shown that under certain conditions, density-dependent dispersal can be destabilizing (Ruxton, 1996; Silva et al., 2001; Silva and Giordani, 2006). By contrast, Ruxton (1994) and Stone and Hart (1999) argued that a weak coupling between chaotic patches can stabilize metapopulations and Ruxton et al. (1997b) subsequently found that also costly dispersal has a stabilizing effect. This result has been questioned by Kisdi (2010), who showed that costly dispersal can also have a destabilizing influence on metapopulation dynamics, using a specific growth function.

Dispersal behaviours relating to arrival and settlement of immigrants in new patches can also affect the stability of metapopulations. Hestbeck (1988) suggested that the social fencing of immigrants by patch dwellers can stabilize dynamics by reducing dispersal-induced oscillations. Immigrants may also choose not to settle in an overcrowded patch because of increased resource competition; this behaviour has been found to stabilize metapopulations (Ruxton and Rohani, 1998). Other behaviours such as conspecific attraction of immigrants and settlement facilitation have been argued to influence metapopulation dynamics as well (Ray et al., 1991; Alvarado et al., 2001).

The previous theoretical studies are based on models using specific functional forms. This restriction of the kinetics in the model is necessary to obtain certain results, such as steady state values of population densities. However, one may ask how the choice of a specific function affects the results. For example, Gross et al. (2004) showed that phenomena such as the paradox of enrichment can be strongly dependent on the particular functional form used in the model. Kisdi (2010) also found that the effect of costly dispersal on stability was dependent on the growth function in use.

Other assumptions are frequently made in order to analyse the stability of metapopulations. Because metapopulations lead to high-dimensional dynamical systems, previous mathematical studies typically reduced their complexity by assuming that dispersal is symmetric or patches are identical. The influence of growth rate heterogeneity between patches has been investigated by Dey et al. (2006), who found that it does not affect stability, even in different spatial topologies. According to this study, the effect of dispersal on the stability of metapopulations is thus not affected by the spatial arrangement of patches.

Here, we investigate the stability of metapopulations using a generalized modelling approach. We introduce a general metapopulation model, which does not assume specific kinetic laws, and encompasses both homogeneous and heterogeneous cases. In the homogeneous case, all patches are identical (as in Ruxton et al., 1997b), whereas in the heterogeneous case, demographic parameters may differ between patches (Dey et al., 2006; Strevens and Bonsall, 2011). The homogeneous case enables us to draw analytical conclusions on the influence of dispersal behaviours such as density-independence, positive and negative density-dependence of dispersal, but also of less studied behaviours such as social fencing, settlement facilitation and conspecific attraction. We also show that for heterogeneous webs the influence of density-independent dispersal on stability is not neutral, but strongly dependent on the topology of the metapopulation.

2. Model

Metapopulations are classically approached using patch-occupancy models, where local population size is ignored, and only the fraction of occupied patches is modelled (Hanski, 1991).

However, deterministic within-patch dynamics models as the one we use here have proven particularly suited to study the influence of dispersal behaviours on metapopulation stability (Taylor, 1990). We consider a metapopulation consisting of M patches and denote the population density in patch i by the scalar X_i . The dynamics of the metapopulation can then be described by the following system of differential equations:

$$\dot{X}_i = G_i(X_i) - L_i(X_i) + \sum_{k=1}^M I_{i,k}(G_i(X_i), G_k(X_k)), \quad (1)$$

where G , L , and I denote potentially non-linear functions governing the local growth, loss, and immigration rates in the respective patches. We distinguish between different immigration terms $I_{i,k}$ originating from different source patches $k \neq i$.

Note that in Eq. (1) the immigration is assumed to depend on the growth rate of the donor patch and not on its density. This choice is directly intuitive for a population with distinct life stages (see for instance Hassell et al., 1995), where only a proportion of the juveniles migrates to other patches. Further, this formulation of the model enables us to segregate competition and dispersal, in accordance with Hassell's criticism of Bascompte and Solé model (Bascompte and Solé, 1994; Hassell et al., 1995). Dispersal of juveniles is a common strategy in ecological populations, especially in animal species such as barnacles or hare (Kent et al., 2003; Bray et al., 2007). In this model immigration is directly dependent on the number of juveniles in the donor patch. This enables us to describe the density-dependence of dispersal, that is a widespread adaptive behaviour in animal populations (Travis et al., 1999).

In the model, immigration is also assumed to depend on the growth rate in the recipient patch, as the number of juveniles of this patch can affect the success of immigration by inhibiting their settlement (Hestbeck, 1988) or facilitating it (Alvarado et al., 2001). The choice of potential patches by immigrants is random as such, only the decision to settle or not depends on growth in recipient patches. Note that when immigrants do not settle in a patch, they could potentially reach other patches and settle there. This would generate a feedback between growth in the potential recipient patch and immigration in other patches, which is not taken into account in our model.

The equation above does not include a term for losses incurred by emigration. Depending on the ecological context emigration losses can be absorbed in either the loss or the gain term that are already included in the equation, by changing the interpretation of these terms accordingly. For instance, consider the scenario where a fixed proportion of juveniles/propagules c leaves the patch to try to settle elsewhere. In this case the losses by emigration were $E = cG(x)$. We can include this loss directly in the growth function of the origin patch, such that we obtain a new growth function $\tilde{G}(x) = (1 - c)G$. Thus emigration losses can be absorbed into the growth function by interpreting the G that appears in the equation as "growth after emigration".

When studying certain questions it is advantageous to absorb the emigration losses in the loss function instead. In particular, this formulation of the model facilitates the interpretation of the immigration function, that is dependent on the growth functions from the donor patches. In this case we interpret the loss function as the sum of all losses, including emigration.

In principle, one could also account for the net effect of emigration and immigration in a single dispersal function. However, this would necessarily lead to negative dispersal terms and interdependency between dispersal terms, both of which are incompatible with the mathematical procedure for stability analysis used below (see Appendix A).

We remark that our model captures each local population only in a single variable and thus does not resolve the age or stage

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