



Short communication

A modified metapopulation model to predict colonisation and extinction rates in fragmented aquatic systems



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ABSTRACT

The construction of a metapopulation model begins with the choice of factors that influence its dynamics. In aquatic environments, and particularly in continental aquatic environments, the variation in the water level is considered a key factor that drives ecosystem functioning and influences local and regional biodiversity. The recent application of the metapopulation approach to aquatic environments has been disappointing. Hence, we present a simple, modified metapopulation model, which combines 'internal colonisation' with 'rescue effect', so that it can be used for identifying the environmental factors that determine the fraction of sites occupied by a given metapopulation. We applied this model to aquatic environments subjected to water level variations, but its application could be extended to any spatially structured population or metapopulation in a fragmented landscape subjected to temporal variations in environmental conditions. We believe that the practical application of this approach is the possibility of manipulating environmental factors to control the fraction of sites occupied by a metapopulation, improving our ability to restore aquatic systems, which is limited by the current metapopulation models.

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1. Introduction

Understanding the spatial and temporal patterns of species distribution and abundance is one major goal of population ecology. A broad theoretical framework has been developed to understand spatial changes in populations, which is also used to put into effect conservation and management plans for endangered species (Soulé and Simberloff, 1986; Hanski, 1998, 2010; Kuussaari et al., 2009). Thus, a metapopulation, i.e., 'a population of populations' (Levins, 1969, 1970), encompasses the local dynamics of recolonisation and extinction in habitat patches connected by migration, and aims at predicting the temporal persistence of a species in a fragmented habitat.

The classical metapopulation approach did not attract much interest of ecologists at first. However, in the late 1980s and early 1990s the fields of evolutionary biology, ecology, and, mainly, conservation biology, showed growing interest in the metapopulation approach. Smedbol et al. (2002) reported that from 1989 to 2000 there was an exponential increase in the number of citations

of the term 'metapopulation'. In addition, Fronhofer et al. (2012) argued that, since the early 2000s, approximately 400 papers based on the metapopulation approach have been published every year.

The use of the classical metapopulation approach has been strongly criticized, because it is mostly theoretical and rarely matches natural systems (Harrison and Hastings 1996; Driscoll et al., 2010; Fronhofer et al., 2012). In the classical metapopulation model, four conditions must be met (Hanski et al., 1995): (i) each discrete habitat patch is able to support a breeding population, (ii) any population may go extinct, (iii) colonisation/recolonisation of empty habitat patches is possible, (iv) and the dynamics of individual populations is asynchronous to allow the persistence of the metapopulation. Thereby, not all spatially structured populations are considered classical metapopulations (e.g., mainland–island, source–sink, patchy, and nonequilibrium metapopulations; Pulliam, 1988; Harrison, 1991). In general, only a few examples in the literature describe classical metapopulations (Hanski et al., 1994; Elmhagen and Angerbjörn, 2001; Baguette, 2004).

Thus, metapopulation models have tried to become more realistic by including variables such as gene flow, local extinction, and spatially correlated dynamics over and above the spatial structure of habitats (Hanski and Gaggiotti, 2004). The intention of

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these models is to predict the dynamics of natural metapopulations through more realistic inferences. Over time metapopulation models have been extended to describe competitive dynamics (as in Hanski and Ranta, 1983), predator–prey relationships (as in Sabelis et al., 1991), and core-satellite species model (as in Hanski and Gyllenberg, 1993). However, most of the advances are still not suitable for the analysis of a real metapopulation, and even more sophisticated mathematical models have been developed. The first of these models were the spatially explicit models proposed by Hanski (1994), named incidence function model (IFM), in which the main structural processes are related to the area of the habitat fragment and landscape connectivity. Recently, stochastic patch occupancy models (SPOM) have been used to assess more realistic metapopulations. These models assume that the habitat occurs in discrete patches surrounded by an unsuitable matrix, in which stochastic environmental and demographic processes are assessed (Lande, 1993; Hanski and Ovaskainen, 2000, 2003).

To begin the construction of a metapopulation model it is necessary to select the factors that influence the dynamics of interest. As we described above, the basic variables in the metapopulation approach are the area and isolation of the habitat fragment. Environmental factors can be also included in the model to enable research on the causes of local extinction and colonisation in fragmented landscapes. Identifying these factors is of great value for conservation programs, because their manipulation can be used in favor or against metapopulations or spatially structured populations (Bellakhal et al., 2014). For example, in aquatic environments, in particular inland aquatic environments, the variation in the water level is considered a key factor that drives ecological functioning and influences local and regional biodiversity patterns (Junk et al., 1989; Thomaz et al., 2007; Lee et al., 2014; Yi et al., 2014). However, the application of the metapopulation approach to these environments has been disappointing (Stelter et al., 1997; Pajunen and Pajunen, 2003; Altermatt and Ebert, 2010). Hence, we provide a new model to investigate the causes of patch colonisation and extinction, and use this new model to look for discrepancies in aquatic environments. Specifically, we present a simple, modified metapopulation model, which combines ‘internal colonisation’ with ‘rescue effect’ (see Gotelli, 2001; pg. 91), so that it can be used in the identification of environmental factors that determine the fraction of sites occupied by a certain metapopulation, and it can be applied to aquatic environments subject to water level variations. We expect that, by showing the connection between water level variations and metapopulation models, we contribute to the understating of colonisation and extinction rates in aquatic environments. A better knowledge of colonisation and extinction rates in aquatic environments allows the elaboration of more realistic plans to restore those environments

2. Development

Our model combines internal colonisation, in which the only source of propagules for metapopulation is the set of sites occupied (Levins, 1970), with the rescue effect, which states that emigrants from surrounding populations reduce the probability of local extinction (Brown and Kodric-Brown, 1977), and can be written as follows (Gotelli, 2001):

$$\frac{dF}{dt} = (i - e)F_t(1 - F_t) \tag{1}$$

where F_t is the fraction of sites occupied at time t , ‘ i ’ is a measure of how much the probability of colonisation of empty sites increases with each additional patch that is occupied, and ‘ e ’ is a measure of strength of the rescue effect.

Through the use of separation of variables, followed by integration of partial fractions, the analytical solution of the differential equation is reached:

$$F_t = \frac{1}{1 + H_0 e^{(e-i)t}} \tag{2}$$

where H_0 is an integration constant related to the initial condition (for $t = 0$, $F_t = F_0$, $H_0 = \frac{1-F_0}{F_0}$). By examining the model above, we see that: (i) if ‘ i ’ > ‘ e ’ and time tends to infinity, the fraction of occupied sites (F) tends to one; (ii) if ‘ e ’ > ‘ i ’ and time tends to infinity, the fraction of occupied sites (F) tends to zero; and (iii) if ‘ e ’ = ‘ i ’, the fraction of occupied sites does not vary. The time for all sites to become occupied ($F = 1$) or not occupied ($F = 0$) depends on the magnitude of the difference between colonisation and extinction rates ($i - e$) (Fig. 1).

However, the difference between ‘ i ’ and ‘ e ’ does not need to behave as a constant, but probably has a deterministic component associated with biotic or abiotic environmental factors and a stochastic component. In a floodplain, for example, the variation in water level acts as a homogenizing factor of the physical, chemical, and biological components (Thomaz et al., 2007). When the water level increases and remains constant for a certain time the species of these environments can disperse to sites that were isolated during periods of low waters. When the water level decreases, the sites will again be isolated and the biological interactions, such as predation and competition will be intensified, along with limiting abiotic conditions. All these factors together will increase the chances that a given species will become excluded from a given site. Therefore, we believe that (i) in periods of low waters, the chance of local extinction is increased; and (ii) in periods of high waters, the chance of colonisation of new sites is increased.

Based on Eq. (2), we can isolate the term ($i - e$) in function of the fraction of sites occupied at time t (F_t) and of the fraction of sites occupied at a later time (F_{t+1}), after a time interval (Δt), reaching the following expression:

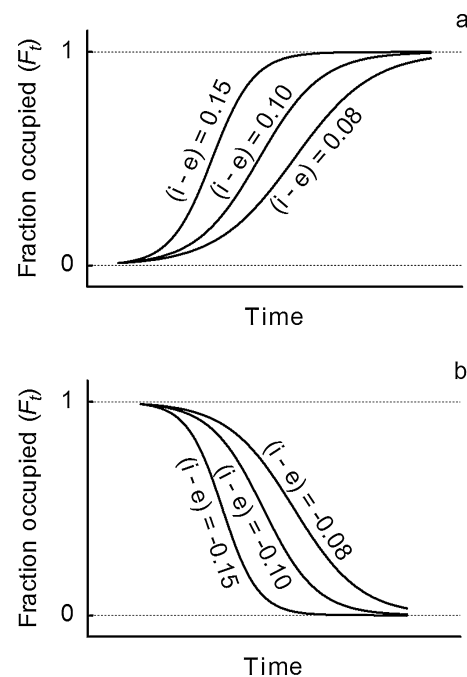


Fig. 1. Simulations over 100 time units of the fraction of sites occupied as a function of the difference between ‘ i ’ (a measure of how much the probability of colonization of empty sites increases with each additional patch that is occupied) and ‘ e ’ (a measure of the strength of the rescue effect). (a) for ‘ i ’ > ‘ e ’ and (b) for ‘ i ’ < ‘ e ’.

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