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Individual variability and metapopulation dynamics: An individual-based model

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ABSTRACT

This paper presents individual-based models describing metapopulation dynamics. The local-population model describes the dynamics of a population without overlapping generations. In each generation, the model follows the individuals' growth. The growth rate of the individuals is affected by the level of resources. The individuals compete for these resources, which are therefore not evenly distributed among them. I compared the persistence of a local population in which the individuals could not disperse with various versions of metapopulation models. Metapopulation models differ in the conditions under which individuals disperse: weaker or stronger competitors, or randomly chosen individuals disperse. Analysis of these models shows that the reasons individuals dispersed affected the persistence of the metapopulation. The influence of the reproduction rate and the individual variability on the persistence of metapopulation is analyzed under the conditions of two types of resource dynamics after the extinction of the local population: with and without regeneration.

1. Introduction

A species may exist in the form of a metapopulation as some number of local populations between which individuals can disperse. Ecologists generally agree that a metapopulation is more stable, persistent or more resistant to invasions than a single local population. This has been confirmed by experiments on systems with different number of species (see Huffaker's (1958) classic paper, and more recent published works, for instance Harrison and Taylor (1997)). Many mathematical models have yielded the same results (Levin, 1974, 1976; Smith, 1972).

Various techniques have traditionally been used in mathematical models to describe the dynamics of metapopulations. Levins's model deals with the proportion of local habitats occupied by local populations (Levins, 1969). Reaction-diffusion models describe changes in the density of populations over time and space (Okubo, 1980). Models based on cellular automata or interacting particle systems take into account that individuals are discrete entities (Tilman et al., 1997; Czárán, 1998; Durett and Levin, 1994a). There are also models classified as individual-based (Hamilton and May, 1977; Ovaskainen and Hanski, 2004; Franhofer et al., 2012). These approaches do not yield the same results (Durett and Levin, 1994b). Nevertheless, they were all constructed on the basis of the same assumption: that dispersing individuals are randomly selected from the local population and they perform a random walk over space. Only in some of these models dispersion probability depends on population density (Ruxton and Rohani, 1998; Travis et al., 1999; Law et al., 2003; Fowler, 2009; Bocedi et al., 2012, 2014).

However, dispersion between local habitats is correlated with higher costs. Therefore, individuals have to have good reasons before they "decide" to disperse. If in local habitats individuals differ in the degree of access to resources (due to social hierarchy or competition), those individuals without sufficient resources to survive and reproduce may decide to disperse to other local habitat in the hope that they will obtain greater resources there. The potential benefit may even outweigh the increased costs associated with dispersion. On the other hand, for those individuals that obtain sufficient resources in their original habitat, dispersion would be an unnecessary risk. Even when dispersing individuals are randomly distributed over space, their decision to disperse can be non-random.

The aim of this paper is to demonstrate that: (1) the dynamics of a metapopulation in which the dispersing individuals are chosen at random differs from the dynamics of a metapopulation in which the dispersing individuals are not chosen randomly, and (2) the dynamics of a metapopulation depends on the rules by which individuals decide to disperse from the local population. In the model presented in this paper the decision to disperse will depend on the amount of resources an individual obtains as the result of intraspecific competition. In theoretical ecology, which is

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dominated by the classical approach, these problems have not yet been considered (Bowler and Benton, 2005). At best, the only problem that has been considered is how the dynamics of a metapopulation depends on the manner in which space is penetrated by migrating animals (Heinz et al., 2006; Hawkes, 2009) or how it depends on constellations of local habitats (Pfenning et al., 2004).

2. The model

2.1. Local population

As a local population model, I used an individual-based model of the dynamics of the number of individuals in a population and their resources (Uchmański, 1999, 2000a,b; Grimm and Uchmański, 2002). It describes the global competition between individuals within a local habitat. An individual perceives the presence of other individuals because they all use a common local pool of resources. Differences in assimilation and reproduction rates among the individuals in the population result from competition. The variability among individuals increases when the level of resources in the local habitat drops. Dispersal in these models will be induced by the condition in the local habitat. These models do not describe species whose individuals go through an obligatory dispersal stage during their life cycle.

The changes of weight w of a single individual isolated from the other individuals are equal to the difference between its assimilation and respiration rates, which are represented by power terms:

$$\frac{dw}{dt} = a_1 w_1^b - a_2 w_2^b \tag{1}$$

When the assimilation rate equals the respiration rate, the weight of the individual is equal to its final value:

$$w_{end} = \left(\frac{a_1}{a_2}\right)^{1/(b_2-b_1)} \tag{2}$$

Eq. (1) describes the growth of an individual when the resources are constant. If the resources V are not constant it can be assumed that b_1 is constant, whereas a_1 varies with V in accordance with the Michaelis–Menten function:

$$a_1 = a_{1,\max} \frac{V}{(V+\delta)} \tag{3}$$

N competing globally individuals affect each other's growth by exploiting a common pool of resources. Let us assume that the individuals compete only once at the start of their life cycle. The value a_1 for an individual now depends not only on V, but also on its initial weight w_0:

$$a_1 = a_1(w_0, V) \tag{4}$$

In the linear function shown at Fig. 1 describing resource partitioning among competing individuals a_1 is defined only for the lowest $w_{0,min}$ and the highest $w_{0,max}$ initial weights in the population:

$$a_1(w_{0,\min}, V) = a_{1,\max} - \frac{\mu}{(V+\delta)} \tag{5}$$

$$a_1(w_{0,\max}, V) = a_{1,\max} \frac{V}{(V+\delta)} \tag{6}$$

The assimilation rate for an individual with initial weights between $w_{0,min}$ and $w_{0,max}$ can be approximated by linear interpolation between the values given by Eqs. (5) and (6). When $V = \infty$, all individuals obtain the same amount of resources, and their assimilation rates are maximal. Differences between individuals arise only if the amount of resources decreases. The values for the parameters δ and μ were chosen so that $a_1(w_{0,min}, V)$ decreases faster than $a_1(w_{0,max}, V)$ when the resources decrease. For a low V, the value for a_1 is

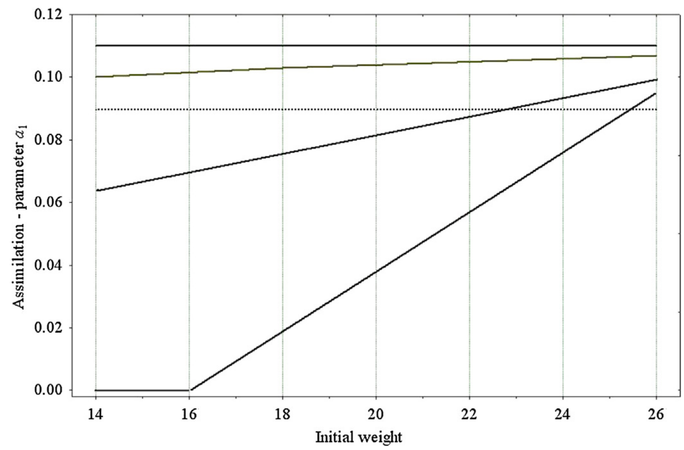

Fig. 1. Resource partitioning among competing individuals in a local habitat in terms of the relationship between the assimilation rate of an individual and its initial body weight. The vertical axis represents the parameter a_1, which is proportional to the assimilation rate. The uppermost horizontal solid line represents partitioning of resources when resources are unlimited. In this case, assimilation is the same for all individuals, regardless of body weight. The solid lines below (looking from the top) represent partitioning of resources for decreasing resources. The lines are constructed so that the assimilation for only the lowest ($w_{0,min} = 14$) and highest ($w_{0,max} = 26$) initial body weights depend on the resources according to Eq. (5) and (6) respectively. The intermediate parts of the curves have been interpolated by drawing straight lines between those extremes. It was assumed that assimilation of the smallest individual decreases more than that of the largest individuals when resources deteriorate. When the pool of resources falls below a certain level, the straight line intersects the horizontal axis. In that case, it was assumed that individuals with a body weight less than the intercept had an assimilation equal to zero. The horizontal dotted line corresponds to the lowest assimilation rate that allows for at least one progeny. Individuals with smaller assimilation rates have no progeny.

positive in Eq. (6), but negative in Eq. (5). The value of a_1 has been assigned zero whenever interpolation yields a negative value for a_1 (Fig. 1). The parameters a_2 and b_2 are independent of the resources and of the influence of other individuals in the population.

Let us assume that the model describes a parthenogenetic population with non-overlapping generations. Individuals reproduce at the end of each generation and die. The number of offspring produced by the ith individual z_i is proportional to the difference between the final weight of the individual and some threshold weight w_{thr}:

$$z_i = Round(c(w_{i,end} - w_{thr})) \tag{7}$$

where parameter c describes the intensity of reproduction. Individuals with a final weight lower than w_{thr} die without reproducing. w_{thr} can be calculated as the fraction λ of the maximum final weight obtained by introducing $a_{1,max}$ into Eq. (2). The initial weights of the progeny for a given individual were selected using a normal distribution with a variance of σ^2 and a mean equal to the initial weight of the individual.

The number of individuals in the next generation N_{t+1} is given by the following equation:

$$N_{t+1} = \sum_{i=1}^{N_t} z_i \tag{8}$$

The amount of resources is constant during a generation. Resources for the next generation were calculated as follows:

$$V_{t+1} = V_t + g - \sum_{i=1}^{N_t} a_{1,i} w_{i,end}^{b1} \tag{9}$$

where g is the constant influx of resources and $a_{1,i} w_{i,end}^{b1}$ is an approximation of the cumulative consumption for an ith