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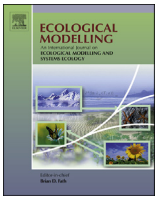

A spatially explicit model to investigate how dispersal/colonization tradeoffs between short and long distance movement strategies affect species ranges

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ABSTRACT

Many organisms can alternatively expand their range through long- and short-distance movements. Understanding the relative importance of these two strategies in determining species range size is of great interest in ecology and conservation biology. The more distant species move, the lower their probability of finding suitable conditions for survival. Thus, a species has a lower probability to succeed in colonization through long-distance dispersal than through short-distance dispersal, i.e., a tradeoff exists between the two strategies. Here, I investigate this issue by using a spatially explicit model where species move from patch to patch across a fragmented landscape. By analyzing the outcomes of 10,000 simulations run on the model under a wide range of tradeoff scenarios, I identified colonization ability as the strongest predictor of species range, followed by short distance dispersal ability, short distance colonization ability and long distance dispersal ability. Thus, range size of species having two different movement strategies is mainly determined by how far the species can move in the short distance strategy, and by its likelihood to succeed in colonization of distant localities, even if the dispersal/colonization tradeoffs between the two strategies are very small.

1. Introduction

There exists a natural relationship between how far a species can disperse, and its odds to succeed in colonization (i.e., in establishing a stable population). In particular, the likelihood of colonization tends to decrease at increasing dispersal distances, as the more distant a species moves from its native range, the lower its probability of finding environmental and climatic conditions suitable for its survival (see, for example, Nathan, 2006; Buston et al., 2012). Although this pattern can be ideally modeled as a long-tailed probability curve (Nathan and Muller-Landau, 2000), its experimental investigation poses several challenges, mostly related to difficulties in measuring dispersal, and in identifying the mechanisms regulating the process of establishment, which is needed to assess colonization likelihood (Nathan, 2001).

This issue is also complicated by the fact that several organisms can have two distinct strategies to expand their range size, sometimes separated in time. Typical examples are found in marine organisms, where several species can be transported by currents for hundreds of kilometers in their larval phase, but then, once settled, are only capable of small movements (James et al., 2002; Shanks et al., 2003; Torda et al., 2013). Most plant species can either colonize contiguous or far areas through different seed dispersal strategies (Nathan et al., 2002), and different range expansion mechanisms (sometimes more than two) can be found in many insects, often associated to wing polymorphism (see, for example, Harrison, 1980; Keller and Holderegger, 2013). For these species, the relationship between dispersal distance and colonization probability can be considered at two different levels, i.e., within and between range expansion mechanisms. In other words, two different dispersal and colonization kernels can be identified for, respectively, the short distance and the long distance movement strategies.

Knowing the roles played by the different strategies in the determination of range size is much relevant in ecology (Caughlin et al., 2014), and conservation biology (Trakhtenbrot et al., 2005), since they clearly relate to the proportion of external vs. autochthonous recruitment which, in turn, is a key aspect in the design and management of networks of protected areas (see, for example, Sala et al., 2002; Planes et al., 2009). In most cases, however, the success in reaching a locality

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and/or colonizing it is strongly affected by chance (especially as regarding for long distance strategies), so that a broad investigation of the ongoing processes is far from experimental reach (Nathan, 2001).

It is commonly assumed that short distance dispersal events affect species geographical ranges more than long distance ones, due to the rarity of the latters (Bolker and Pacala, 1999; Harries and Clement, 2014). Yet long distance dispersal events may be more common than usually thought (Alsos et al., 2007; Anderson et al., 2011), and various authors claim that occasional long-distance jumps may be more effective in expanding species ranges and connecting isolated populations than numerous short distance dispersal events (Trakhtenbrot et al., 2005; Nathan, 2006; Pergl et al., 2011; Gillespie et al., 2012; Keller and Holderegger, 2013; Caughlin et al., 2014). This suggests that the frequency balance between short and long distance movement events is likely to have a stronger effect on species ranges than fine differences between the dispersal and colonization kernels within the two movement strategies.

Tradeoffs exist in dispersal and colonization ability between the short and long distance movement strategies. For example, larvae of marine organisms have a good chance to reach distant areas, but are also subjected to very high mortality before settlement (Vaughn and Allen, 2010). This pattern is reversed for adult individuals, that have less chances to reach a far locality, but are more likely to succeed in colonization (Frisk et al., 2014). Here I use a spatially explicit model to show how investigating the effects of these tradeoffs on species ranges can improve our understanding of range expansion mechanisms.

2. Methods

2.1. Model overview

Each model runs in a single fragmented landscape, which is generated by randomly positioning isolated patches in a Cartesian plane. A random value ($Sp_{\max}$) is associated to each patch, indicating the maximum number of species the patch can host. The dispersal kernel, i.e., the function describing the probability of a species to disperse from patch i to patch j is given by:

$$D_{ij} = \left(\frac{1-d_{ij}}{d_{\max}}\right)^{\alpha},$$

where d_{ij} is the Euclidean distance between patch i and patch j, $d_{\max}$ is the distance between the two farthest points in the landscape, and α is the dispersal coefficient for the species under study. The response of D_{ij} to variations in the ratio $d_{ij}/d_{\max}$ for different values of α is shown in Fig. 1.

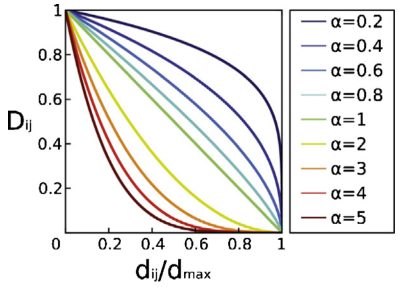

Fig. 1. Response of species dispersal kernel, i.e., the function describing the species' probability to disperse from patch i to patch j, given by $D_{ij} = (1-d_{ij}/d_{\max})^{\alpha}$, to variations in the dispersal coefficient α. The parameter d_{ij} indicates the Euclidean distance between patch i and patch j, while $d_{\max}$ is the distance between the two farthest points in the landscape.

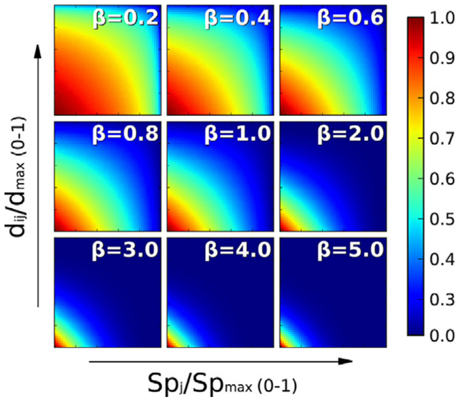

Fig. 2. Response of species colonization kernel, i.e., the function describing the probability of a species coming from patch *i* to succeed in colonizing patch *j*, given by $C_{ij} = [(1-Sp_j/Sp_{\max}) \times (1-d_{ij}/d_{\max})]^{\beta}$, to variations in the colonization coefficient β (see Section 2). The color scale indicates the values of C_{ij}. The parameter d_{ij} indicates the Euclidean distance between patch i and patch j, $d_{\max}$ is the distance between the two farthest points in the landscape, Sp_j is the number of species already present in the *j*-th patch, and $Sp_{\max}$ is the maximum number of species the j-th patch can host.

The probability that a species, after having reached a patch, successfully colonizes it takes into account both the number of species already present in the patch, according to the classical MacArthur and Wilson (1967) model, and the distance between the arrival and the departure patches. The first aspect accounts for resource availability, while the second takes care of the fact that the farther a species moves, the lower are its chances to find favorable climatic/environmental conditions (i.e., conditions similar to those of the departure patch). Thus, the colonization kernel, i.e., the function describing the probability of a species coming from patch i to successfully colonize patch j is given by:

$$C_{ij} = \left[\left(\frac{1-Sp_j}{Sp_{\max}}\right) \times \left(\frac{1-d_{ij}}{d_{\max}}\right)\right]^{\beta},$$

where Sp_j is the number of species already presented in the j-th patch, $Sp_{\max}$ is the maximum number of species the j-th patch can host, and β is the colonization coefficient for the species under study. The response of C_{ij} to variations in the ratios $Sp_j/Sp_{\max}$ and $d_{ij}/d_{\max}$ for different values of β is illustrated in Fig. 2.

2.2. Model functioning

The model runs as follows:

1) A landscape is generated by placing at random N patches (with N being extracted with uniform probability from the interval [500,1500]) in a Cartesian plane. The boundaries of the Cartesian plane are set as N × X for the *x*-axis, and N × Y for the *y*-axis, with both *X* and Y extracted at random from the interval [50,100]. Each patch is populated with an initial set of species extracted at random from the species pool (see point 2), having size equal to 1% of $Sp_{\max}$ of that patch. This value is rounded to the nearest integer, thus the initial set of species is empty for patches having $Sp_{\max}$ smaller than 50. An example of random landscape is provided as Supplementary material (Fig. S1).
2) A set including a random number of species (SpN) varying between 500 and 1500 is generated. It should be highlighted that this set includes only the species of interest, i.e., a set of species having both a short and a long distance dispersal strategy. Nonetheless, the model considers the presence of other species, which contribute to turnover and compete for resources (see also points 4 and 5).