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Evolution of dispersal distance: Maternal investment leads to bimodal dispersal kernels



Emanuel A. Fronhofer^{a,b,*}, Hans Joachim Poethke^b, Ulf Dieckmann^c

^a Eawag: Swiss Federal Institute of Aquatic Science and Technology, Department of Aquatic Ecology, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland

^b Field Station Fabriktschleichach, University of Würzburg, Glashüttenstr. 5, D-96181 Rauhenebrach, Germany

^c Evolution and Ecology Program, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria

HIGHLIGHTS

- It is unclear what shape evolutionarily stable dispersal kernels have.
- The evolution of dispersal kernels is examined in an individual-based simulation.
- We model distance-dependent competition, dispersal costs, and maternal investment.
- Competition and dispersal costs lead to unimodal kernels.
- Maternal investment selects for bimodal kernels and long-distance dispersal.

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ABSTRACT

Since dispersal research has mainly focused on the evolutionary dynamics of dispersal rates, it remains unclear what shape evolutionarily stable dispersal kernels have. Yet, detailed knowledge about dispersal kernels, quantifying the statistical distribution of dispersal distances, is of pivotal importance for understanding biogeographic diversity, predicting species invasions, and explaining range shifts. We therefore examine the evolution of dispersal kernels in an individual-based model of a population of sessile organisms, such as trees or corals. Specifically, we analyze the influence of three potentially important factors on the shape of dispersal kernels: distance-dependent competition, distance-dependent dispersal costs, and maternal investment reducing an offspring's dispersal costs through a trade-off with maternal fecundity. We find that without maternal investment, competition and dispersal costs lead to unimodal kernels, with increasing dispersal costs reducing the kernel's width and tail weight. Unexpectedly, maternal investment inverts this effect: kernels become bimodal at high dispersal costs. This increases a kernel's width and tail weight, and thus the fraction of long-distance dispersers, at the expense of simultaneously increasing the fraction of non-dispersers. We demonstrate the qualitative robustness of our results against variations in the tested parameter combinations.

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1. Introduction

Within the boundaries of local adaptation a species' range is mainly influenced by its dispersal abilities (Kokko and López-Sepulcre, 2006; Kubisch et al., 2014). Consequently there are numerous empirical and even more theoretical studies on dispersal of plants and animals (Clobert et al., 2012). Yet, so far, particularly theoretical studies on dispersal have mainly focused on the emigration propensity of individuals, while the dispersal

process itself and the question how far to disperse has been mostly ignored or tackled with rather arbitrary assumptions like nearest neighbor (e.g. Travis et al., 1999; Gros et al., 2006) or global dispersal (e.g. Poethke and Hovestadt, 2002). However, the growing awareness of the enormous influence of dispersal distances on colonization and range expansion particularly in plants (Nichols and Hewitt, 1994; Bohrer et al., 2005; Nathan, 2006) has inspired a more thorough analysis of so-called dispersal kernels – the statistical distribution of propagules in terms of distances travelled from their origin (Cousens et al., 2008; Hovestadt et al., 2012). The specific form of such kernels defines not only the mean dispersal distance, but also the occurrence of potentially important but rare long-distance dispersal events (LDD; Kot et al., 1996;

* Corresponding author.

E-mail address: emanuel.fronhofer@eawag.ch (E.A. Fronhofer).

Muller-Landau et al., 2003). ‘Fat-tailed’ distributions, which imply a relatively large proportion of LDD, increase the velocity of species invasions (Kot et al., 1996; Caswell et al., 2003), their ability to cope with habitat fragmentation (Dewhurst and Lutscher, 2009), and may influence biogeographic patterns of species diversity (Chave et al., 2002; Nathan, 2006).

An additional challenge arises from the term ‘dispersal kernel’ not always being clearly defined. A kernel may be described by two distinctly different probability-density functions (pdfs): (i) the density pdf, which describes the density of propagules to be expected at a certain distance, and (ii) the distance pdf, which describes the distribution of distances the propagules are dispersed to (Cousens et al., 2008; Hovestadt et al., 2012). While both definitions are correct and kernels can be expressed either way, their shapes will differ systematically. For example, if one considers a uniform distribution of propagules per area up to a certain maximal dispersal distance, the density pdf will resemble a cylinder, while the distance pdf will be a linearly increasing function of distance up to the maximal dispersal distance. This is simply due to the fact that in two dimensions the area of a circle increases quadratically with its radius, so the area of a thin ring at the circle’s perimeter increases linearly with its radius. Thus, if the propagule density is to be constant within each ring independent of its radius, proportionally more propagules have to be dispersed to larger distances, so as to yield the same propagule density for larger rings. Throughout this article, we express dispersal kernels in terms of their distance pdf.

In spite of the relevance of the specific form of the dispersal kernel for determining the distribution of propagules in space, it is still unclear what an evolutionarily stable kernel should look like. This question was first addressed by Hovestadt et al. (2001), who found that fat-tailed dispersal kernels evolve in autocorrelated landscapes (and at sufficiently fine scales, all landscapes are autocorrelated). While a certain fraction of propagules will disperse to the immediate surroundings of the parent, a significant fraction of propagules will exhibit long-distance dispersal: the latter propagules disperse more or less uniformly over the landscape, which minimizes kin competition (Hamilton and May, 1977; Rousset and Gandon, 2002). The shape of the dispersal kernel can thus be understood as the result of two opposing selection pressures: kin competition would be minimized by a completely uniform distribution of propagules, while distance-dependent dispersal costs (for a recent review see Bonte et al., 2012) select against long-distance dispersal. While not considered here, other mechanisms, such as inbreeding avoidance, that have been analyzed in the context of dispersal rate evolution (Clobert et al., 2012) may also influence dispersal distances (but see Bitume et al., 2013).

While Hovestadt et al. (2001) include dispersal costs only implicitly, via an assumption of increasingly unsuitable habitat Rousset and Gandon (2002) explicitly analyzed the effect of distance-dependent dispersal costs. Like most studies on dispersal evolution Rousset and Gandon (2002) assume that dispersal is under the control of the dispersing individual. Yet, this assumption is rather unlikely to be completely true for passively dispersing propagules like seeds. Thus, Starrfelt and Kokko (2010) studied the evolution of dispersal distance and kernel shapes in the context of parent–offspring conflict. They could show that maternal control of dispersal generally leads to longer dispersal distances and even to fat-tailed kernels.

While all these earlier studies represent important steps towards a better understanding of the evolution of the shape of dispersal kernels, two fundamental issues known to heavily influence dispersal evolution have only rarely been taken into account: (i) effects of the overall strength, and gradual attenuation with distance, of competitive interactions are understudied (see

Bolker, 2010, for a study that does take these effects into account), and (ii) effects of trade-offs in parental investment into offspring dispersal have not been investigated. Firstly, as Berger et al. (2008) point out, competition is a process that fundamentally shapes the spatial patterns found in plant communities and that needs to be modelled at the individual level (Law et al., 2003; Travis et al., 2010; North et al., 2011), and not only at the population level. A large number of models in dispersal ecology are grid-based (Murrell et al., 2002; Gros et al., 2006; Bonte et al., 2010), which implies either that competition acts at the local population level, or – if only one individual is allowed per grid cell – that the assumed competition kernel has a quadratic base, which is a somewhat artificial assumption. Secondly, if one concedes that in passive dispersers the dispersal process, more specifically the dispersal distance, is centrally influenced by the parent organism (‘maternal control’ as in Starrfelt and Kokko, 2010) it is also very likely that parents will invest in the dispersal abilities of their offspring (Wheelwright and Logan, 2004). It has been shown theoretically and empirically (Roff, 1994; Fronhofer et al., 2011; Burton et al., 2010; Travis et al., 2010, 2012) that life-history trade-offs, e.g., between reproduction and dispersal ability, may deeply influence the evolution of dispersal, in a way that may lead, for example, to polymorphisms in which low-dispersal and high-dispersal morphs coexist. In the context of sessile organisms with passive dispersal, such trade-offs are inter-generational and are more appropriately described in terms of maternal investments that may offset an offspring’s dispersal costs. Especially in plants, in which seeds are surrounded by maternal tissue and may depend on these structures for dispersal, it is sensible to include this aspect and to analyze the consequences of such maternal investment.

Therefore, we here present an individual-based model of a population of sessile organisms, such as trees or corals, and investigate the evolution of the shape of dispersal kernels. In contrast to the great majority of existing models (e.g. Murrell et al., 2002; Gros et al., 2006; Bonte et al., 2010; Bolker, 2010; North et al., 2011), we do not *a priori* assume any specific kernel shape. Assuming that the kernel belongs to a certain family of distance functions can lead to erroneous evolutionary attractors (for a discussion see Dieckmann and Metz, 2006). Instead, we derive evolutionarily stable kernel shapes under the assumption that long-term evolution can find ways to realize them. We explicitly account for three different selection pressures of potential relevance for the evolution of the shape of dispersal kernels: distance-dependent competition (Roughgarden, 1974; Law et al., 2003; Travis et al., 2010; North et al., 2011), distance-dependent dispersal costs (Bonte et al., 2012), and maternal investment reducing the dispersal costs experienced by dispersing offspring (Herrera, 1995; Travis et al., 2010).

2. The model

In our model, each individual ($i = 1, \dots, N$) is characterized by its location (x_i, y_i) and its dispersal kernel (P_i). Individuals are located in a two-dimensional spatially continuous and homogeneous habitat, with $0 \leq x_i, y_i \leq 100$ and periodic boundary conditions. Time is discrete and generations are overlapping.

2.1. Dispersal kernels

We define dispersal kernels as probability distributions ($P(d)$) of reaching a distance (d) after a dispersal event, i.e., we use a distance pdf. Since we do not *a priori* restrict attention to a specific functional relationship between P and d , the dispersal kernels in our model are implemented as function-valued traits (Dieckmann

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