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



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## 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;

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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

et al., 2006). As is common in studies of function-valued traits, we approximate the theoretically infinite-dimensional trait by a sufficiently large, but finite, number of values. Specifically, we use  $n=21$  values to describe the probabilities of reaching a distance class ( $d_k, k=1, \dots, n$ , with  $d_1$  corresponding to  $d=0$ ,  $d_2$  corresponding to  $0 < d \leq 1$ ,  $d_3$  corresponding to  $1 < d \leq 2$ , ..., and with  $d_{21}$  corresponding to  $19 < d \leq 20$ ). All values  $P(d_k)$  are positive and are normalized so as to sum up to 1,  $\sum_{k=1}^n P(d_k) = 1$  (for similar models see Hovestadt et al., 2001; Starrfelt and Kokko, 2010; Fronhofer et al., 2014).

To ensure that the chosen trait discretization does not unduly influence our results, we carried out additional numerical analyses with up to  $n=31$  distance classes. We also analyzed the effect of increasing the extent of the first distance class (with  $d_1$  corresponding, instead of to  $d=0$ , to  $0 \leq d \leq 0.1$  or to  $0 \leq d \leq 0.2$ ). These robustness checks are discussed in detail below; here we only mention that our results remained essentially unchanged.

## 2.2. Reproduction

Once per time step, all individuals reproduce sexually. They produce a stochastic number of offspring, drawn from a Poisson distribution with mean  $\lambda$ . As our model is applicable, for example, to trees, we assume that individuals are simultaneously monoecious, i.e., they have male and female reproductive organs. Selfing is excluded, and for simplicity we assume that an individual mates with its nearest neighbor as in Starrfelt and Kokko (2010).

We have tested the robustness of our results in scenarios with global random mating. Note that kin structure, which is known to be highly relevant for dispersal evolution and especially in the context of dispersal distances (Hamilton and May, 1977; Rousset and Gandon, 2002), is significantly reduced by such a mating strategy. Results are reported in the supporting information figure S1. Even in this extreme scenario the effect of maternal investment is still visible. Clearly, as one would expect due to the altered kin structure, the magnitude of the effects are reduced.

## 2.3. Inheritance

As our model is phenotypic, offspring inherit for each distance class of their dispersal kernel the mid-parental value of their two parents, altered by a segregation kernel (Roughgarden, 1979). The latter is given by a normal distribution with the mid-parental value as mean and  $\sigma_s = 0.1$  as standard deviation. This allows us to include the effects resulting from the processes of segregation and recombination during meiosis.

We additionally assume rare mutation events. The per locus mutation rate is constant ( $m=0.001$ ). To optimize computing time, the root-mean-square size of mutational steps, i.e., the average amount by which a value  $P_i(d_k)$  is changed by mutation decreases with time (Poethke et al., 2010):  $\sigma_m = e^{-5t/t_{\max}}$ , with  $t$  denoting time and  $t_{\max}$  the maximal time considered in a model run. To guarantee that segregation, recombination and mutations result in positive numbers for the kernel the values are log-transformed before the mid-parent values are altered by the segregation kernel and mutations. Mutations are applied after segregation, with mutational increments being drawn from a normal distribution with zero mean and standard deviation  $\sigma_m$ .

## 2.4. Dispersal

As we investigate the evolution of the dispersal kernel of sessile organisms with passive dispersal, we assume maternal control of dispersal (see e.g. North et al., 2011). This means that the mother's genotype defines the dispersal distance of the offspring. As Hamilton and May (1977) note, optimal dispersal strategies may

be different depending on whether one maximizes the inclusive fitness of the mother or of the offspring. Due to costs of dispersal applying directly to the offspring, dispersal under offspring control is often reduced. This has been analyzed in detail by Starrfelt and Kokko (2010). We have run additional numerical analyses with offspring control and found that the results corresponded well to their results.

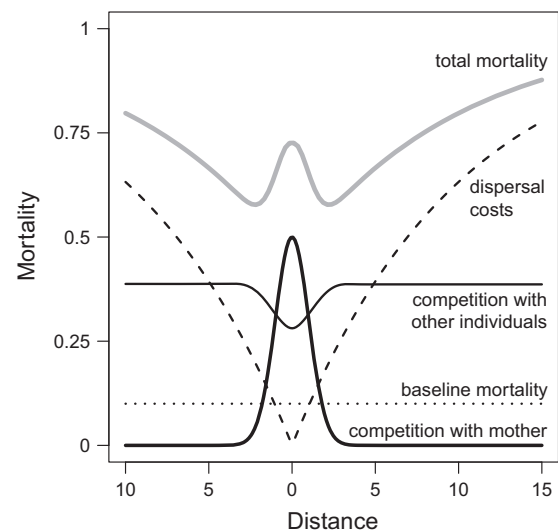
The dispersal distance of an offspring is determined by randomly drawing a distance class ( $d_k$ ) according to the maternal dispersal kernel ( $P(d_k)$ ). The realized dispersal distance is drawn randomly with a uniform distribution from this interval, i.e., if  $d_1$  is drawn the dispersal distance ( $d$ ) is always zero, if  $d_2$  is drawn the dispersal distance is between 0 and 1 ( $0 < d \leq 1$ ) and so forth.

## 2.5. Dispersal costs and maternal investment

As we assume a constant per step mortality ( $\mu_d^0$ ) the probability of dying while dispersing over a given distance ( $\delta$ ) follows an exponential function (Fig. 1; see also Fronhofer et al., 2014):

$$\mu_d = 1 - e^{-\mu_d^0 \delta}. \quad (1)$$

Of course, the experienced dispersal costs will not depend on the net distance travelled, but on the realization of the dispersal event. Logically, Eq. (1) holds for a straight line walk. For any other realization the cost function will follow the general form  $\mu_d = 1 - e^{-\mu_d^0 \delta^v / c}$ . If the realization is a (correlated) random walk, i.e. follows a Lévy process, we find that  $v < 1$  (results not shown). This does not change the shape of the dispersal cost function qualitatively:  $v < 1$  increases the slope of the function for small distances while it saturates later. Additional numerical analyses show that our results are not influenced qualitatively by this assumption. For a detailed analysis of the influence of different dispersal cost functions see Rousset and Gandon (2002).



**Fig. 1.** The components of mortality. Dispersal costs ( $\mu_d$ , dashed line) increase asymptotically with distance (Eq. (1), function shown for 'offspring pay' scenario). In addition we assume a distance- and density-independent, constant baseline mortality ( $\mu_0$ , dotted line). The shape of the competition kernel, is very flexible and can vary from leptokurtic to platykurtic ( $\gamma$ , see Eq. (4) and text for details, thick black line). Competition with other individuals than the focal individual (e.g. a mother tree) shows a minimum at the location of the focal individual (thin black line; data taken from numerical analyses; smooth spline regression over the mean of 100 focal individuals of age  $a=3$  for each of 20 replicate simulation runs; smoothing parameter:  $\lambda = 0.3$ ). The resulting total mortality a dispersing propagule experiences is depicted in grey. Note that mortality is a probability and the components therefore cannot be summed up directly. Parameters:  $\gamma = 2$ ,  $\sigma = 1$ ,  $a=3$ ,  $H_a = 3$ ,  $\mu_d^0 = 0.1$ ,  $\lambda_0 = 4$  (for the numerical analyses).

Dispersal costs may be offset by maternal investment which increases the dispersal ability of propagules (see also Travis et al., 2010). More specifically our model assumes that an increase in dispersal ability is correlated with a decrease in fertility (Zera and Denno, 1997; Tanaka and Suzuki, 1998; Roff, 2002; Roff et al., 2002). For simplicity we will assume two extreme scenarios: (i) either the offspring carry all costs as described above (Eq. (1); scenario ‘offspring pay’) or (ii) the costs are completely covered by maternal investment (scenario ‘mother pays’). To keep both scenarios comparable we determine the maternally covered, kernel-dependent, costs by summing up the distance-dependent costs over the entire kernel ( $P(d_k)$ ) for all possible distance classes ( $d_k$ ):

$$\tau = \sum_{k=1}^n \mu_d(d_k)P(d_k). \quad (2)$$

Costs trade-off with fecundity (Burton et al., 2010; Fronhofer et al., 2011) and the mean number of offspring is then calculated as

$$\lambda = \lambda_0(1 - \tau), \quad (3)$$

with  $\lambda_0 = 4$  as our default choice (see supporting information S2 for a sensitivity analysis).

Note that in order to analyze the influence of relaxing this strong assumption of either ‘mother pays’ or ‘offspring pay’ we ran two classes of additional numerical analyses. Firstly, we show that if both, mother and offspring, have to pay dispersal costs our results hold in principle although effects are reduced due to shared costs (supporting information S3). Secondly, we allowed the allocation of costs to be itself an evolvable trait: depending on this trait a proportion of the distance dependent dispersal costs ( $\mu_d^0$ ) is paid by the mother according to Eq. (2) and the remaining costs are paid by the offspring (Eq. (1)). For all tested parameter combinations (Table 1) no intermediate cost allocation strategy evolved and the evolutionarily stable strategy was full maternal investment, i.e. ‘mother pays’ (see supporting information S4).

## 2.6. Competition and mortality

We assume that the strength of competitive interactions (e.g., for space, light, or nutrients) depends on inter-individual distances. In addition and in contrast to previous models that assume annual organisms with non-overlapping generations (Travis et al., 2010; North et al., 2011) we include age-dependence since competition will be asymmetric between established trees and seedlings, for example. In our model, competition acts by increasing mortality, and not by decreasing fertility (Fig. 1). This allows us to derive a density-dependent individual mortality term, i.e. the probability of dying in the present time step ( $\mu_i$ ). For the form of this competition kernel – often termed zone or sphere of influence (Berger et al., 2008) – we assume a general and very flexible functional relationship (Roughgarden, 1974). This approach is similar to the sphere of influence model presented by Schiffrers et al. (2011). The effect of an individual  $j$  on the focal

individual  $i$  is calculated as

$$\mu_{ij} = e^{-(\Delta_{ij}/f)^\gamma} \frac{a_j}{a_j + H_a}, \quad (4)$$

with  $f = \sigma \sqrt{\Gamma(1/\gamma)}/\sqrt{\Gamma(3/\gamma)}$ , where  $\Gamma$  is the gamma function. The first term of the function reflects distance- and the second term age-dependence.  $\Delta_{ij}$  is the Euclidean distance between individuals  $i$  and  $j$ .  $\sigma$  is the standard deviation of the competition kernel and  $\gamma$  determines its kurtosis:  $\gamma = 2$  yields a normal (mesokurtic) distribution,  $\gamma < 2$  a leptokurtic distribution (narrow peak and fat tails), and  $\gamma > 2$  a platykurtic distribution (wide peak and thin tails). The kurtosis parameter (with  $\gamma = 2$  as our default choice) thus determines the balance between localized competition and long-range competition, while the standard deviation (with  $\sigma = 1$  as our default choice) scales the width of the competition kernel.

Age-dependence is a simple asymptotic function with  $a$  as the age of individual  $j$  and  $H_a$  as the half-saturation constant, i.e. the age at which an individual reaches half of its maximal competitive ability (with  $H_a = 3$  as our default choice). Note that the age-dependent term is important since without it competition between adults and young offspring is symmetric.

The total competition related mortality ( $\mu_i$ ) of individual  $i$  may additionally include a baseline mortality ( $\mu_0 = 0.1$  as a standard value) which is density independent:

$$\mu_i = 1 - (1 - \mu_0) \prod_{i \neq j} (1 - \mu_{ij}). \quad (5)$$

See Fig. 1 for a summary of all mortality components. This figure includes the effects of all individuals in a landscape as in Eq. (5) and additionally illustrates the dominant effect of the focal individual.

## 2.7. Numerical analyses

Depending on parameter combinations population sizes varied roughly between 400 and over 7000 individuals. The dispersal kernels were initialized as uniform distributions with some additional random variation (random number drawn from a uniform distribution between  $-0.1$  and  $0.1$  before normalization). Computing time was set to  $t_{\max} = 10,000$  time steps, a time span that allowed all model runs to reach equilibrium (this was usually the case after approx. 5000 time steps). The results shown below are means over 25 replicates. See Table 1 for a summary of relevant parameters and tested values.

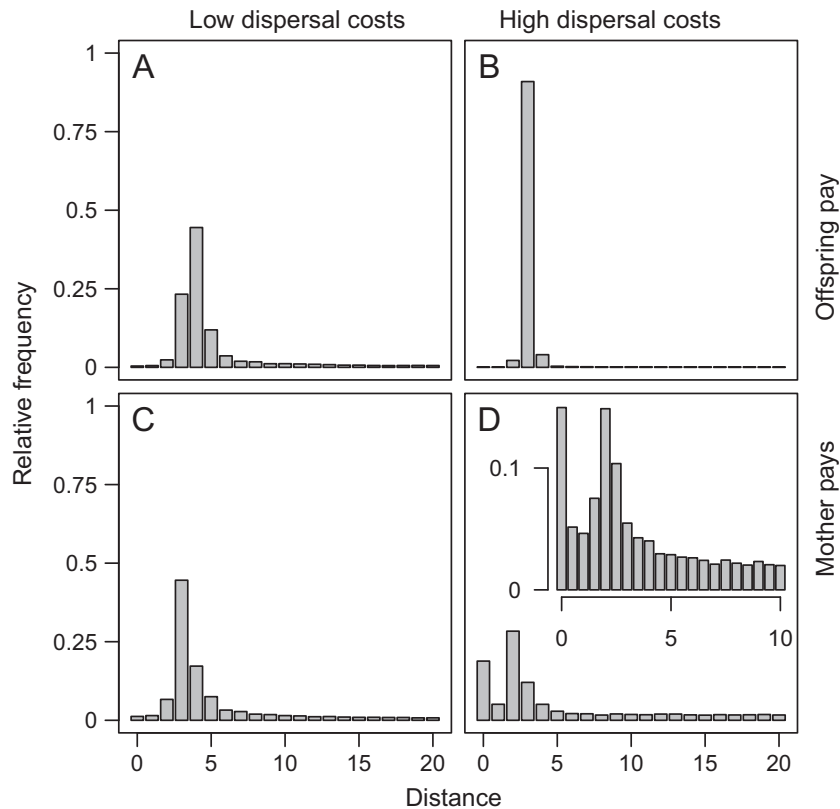
## 3. Results

### 3.1. Evolution of dispersal kernels

In all scenarios without maternal investment, i.e. when the offspring pay distance-dependent dispersal costs according to Eq. (1), we find that the evolutionarily stable dispersal kernel is unimodal (Fig. 2A). This results from the interaction between the competition kernel, competition with related dispersers and

**Table 1**  
Important model parameters, their meaning and tested values.

Parameter	Values	Meaning
$\lambda_0$	2, 4, 8	Fecundity
$\mu_0$	0.05, 0.1, 0.2	Baseline mortality (density independent)
$\sigma$	0.5, 1, 2	Width of the competition kernel (standard deviation)
$\gamma$	1, 2, 4	Kurtosis of competition kernel
$H_a$	1.5, 3, 6	Age-dependence of competition (half-saturation constant)
$\mu_d^0$	0.05, 0.1, 0.15, ..., 0.4	Dispersal costs (per distance unit)



**Fig. 2.** Maternal investment and the evolution of dispersal kernels. All four panels show evolutionarily stable dispersal kernels (distance pdfs). The upper row (A, B) depicts the influence of dispersal costs without maternal investment, i.e. when offspring pay distance-dependent dispersal costs according to Eq. (1). The competition kernel (Eq. (4)) leads to unimodal distributions (A). Increasing dispersal costs lead to narrower and more peaked kernels (B). The lower row (C, D) shows kernels for scenarios with maternal investment, i.e. the mother pays kernel-dependent dispersal costs (Eq. (2)) and reduces her fecundity in order to maximize offspring survival during dispersal (Eq. (3)). Maternal investment leads to relatively more fat-tailed kernels in comparison to the 'offspring pay' scenario and to bimodality at high dispersal costs (D). The inset in panel D shows the same numerical analysis for an increased resolution of the dispersal kernel (distance class extent of 0.5 instead of the default of 1). Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.1$  (left panels; A, C) or  $\mu_d^0 = 0.4$  (right panels; B, D). See supporting information figure S8 for the equivalent density pdfs.

dispersal costs (see Fig. 1). Increasing dispersal costs lead to narrower, more peaked and less fat-tailed kernels (Fig. 2B). This is due to an increase in the slope of the dispersal cost function (Fig. 1).

### 3.2. Maternal investment leads to bimodal kernels

In general, maternal investment increases the occurrence of LDD, i.e. the weight of the kernel's tail (Fig. 2). Interestingly, maternal investment inverts the effect of dispersal costs on long-distance dispersal: here increasing dispersal costs lead to an increase in tail weight (Fig. 2D). In addition, the evolutionarily stable dispersal kernel for high dispersal costs is bimodal (Fig. 2D) with an important proportion of propagules remaining very close to the maternal individual and a mass of offspring showing LDD. The inset in Fig. 2D shows the same numerical analysis for an increased resolution of the dispersal kernel (distance class extent of 0.5 instead of the default of 1). Note that the bimodality we describe here occurs at the individual level and is not the result of a mixed strategy with coexisting short- and long-distance dispersers (supporting information S5).

### 3.3. Dispersal costs

A more detailed analysis of the influence of dispersal costs shows that, as one would assume, the mean dispersal distance decreases with costs in the 'offspring pay' scenario (Fig. 3A). Yet, with maternal investment ('mother pays') the relationship becomes u-shaped, i.e. higher dispersal costs favor higher mean dispersal distances (Fig. 3A).

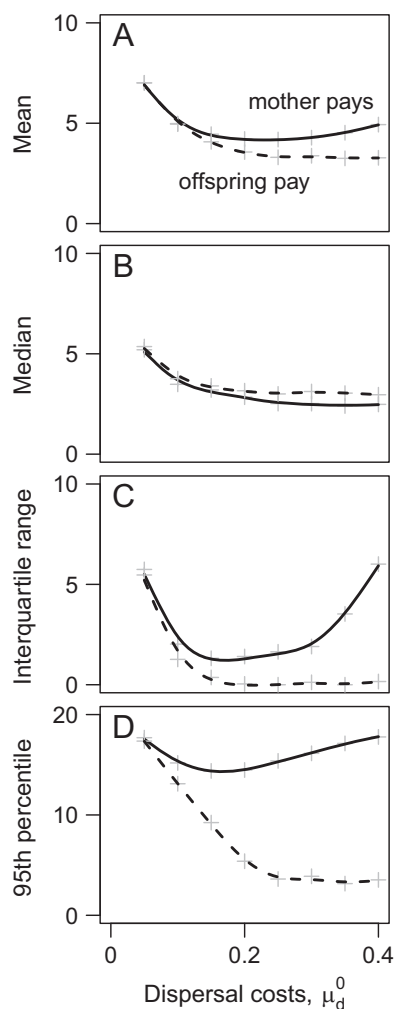
Clearly, this is due to the asymmetry and tail weight of the kernels (Fig. 2) since the median dispersal distance decreases monotonically with dispersal costs (Fig. 3B). The median reaches a steady value which is defined by the width of the competition kernel (see also Fig. 4). The scenario assumed, i.e. distance costs paid by the offspring ('offspring pay') vs. kernel costs paid by the mother ('mother pays'), does not influence the median dispersal distance.

As mentioned above, increasing dispersal costs lead to narrower kernels if the offspring pay distance dependent dispersal costs (Fig. 3C). However, in the case of maternal investment this tendency is reversed for sufficiently high dispersal costs (Fig. 3C; here  $\mu_d^0 > 0.2$ ) which is due to the above described bimodality (Fig. 2D).

A similar pattern can be observed for tail weight (Fig. 3D). In the 'offspring pay' scenario increasing dispersal costs reduce tail weight, here measured as the 95th percentile of the kernel. Maternal investment inverts this pattern: as soon as the kernel becomes bimodal its tail weight increases with dispersal costs (Fig. 3D).

### 3.4. Shape of the competition kernel

The qualitative results presented above, i.e. the emergence of relatively more fat-tailed and bimodal kernels in scenarios with maternal investment, are robust against variation in all model parameters (Fig. 4 and supporting information S2). Not surprisingly, the width of the competition kernel influences the mean and the median of the dispersal kernel, i.e. the location of the peak (Fig. 4A,B). Wider competition kernels, i.e., higher values of the standard deviation ( $\sigma$ ), lead to bimodal dispersal kernels at lower dispersal costs in the 'mother pays' scenario (Fig. 4C,D). The



**Fig. 3.** Maternal investment and dispersal costs. The graphs represent a systematic analysis of the influence of dispersal costs ( $\mu_d^0$ ) on mean (A), median (B), interquartile range (C) and the position of the 95th percentile (D) of the evolutionarily stable dispersal kernels. Here and in the following figures the solid line represents results for scenarios with maternal investment ('mother pays') and the dashed line without ('offspring pay'). For 'mother pays' scenarios the mean dispersal distance shows a u-shaped relation with increasing dispersal costs while the median does not (A, B). The interquartile range (C) captures the emerging bimodality in 'mother pays' scenarios. The 95th percentile is a good indicator for fat tails (D). Parameter values:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ . The grey crosses represent data points and the lines are smooth spline regressions (smoothing parameter:  $\lambda = 0.3$ ).

pattern is not lost for narrower competition kernels, yet requires higher dispersal costs to emerge ( $\mu_d^0 > 0.5$ ; not shown).

The kurtosis of the competition kernel ( $\gamma$ ) has only very slight effects. More leptokurtic shapes lead to slightly smaller dispersal distances (Fig. 4E,F) because the costs inflicted by competition decrease at a faster rate at small distances. As a consequence more platykurtic competition kernels lead to bimodality in 'mother pays' scenarios at lower dispersal costs (Fig. 4G) and to more LDD (Fig. 4H).

The shape, especially the height of the competition kernel, also depends on the focal individual's age (Eq. (4)). We find that the slower an individual's competitive ability increases ('slow growth' in Fig. 4; larger values of the half-saturation constant  $H_a$ ) the smaller dispersal distances become (Fig. 4I,J). Under such conditions the usual pattern of higher dispersal distances in scenarios with maternal investment is inverted (Fig. 4J) which is due to a more pronounced bimodality (Fig. 4K) with a higher peak at distance zero. This is primarily due to the lower competitive ability of a focal maternal individual. In turn, this pattern interacts

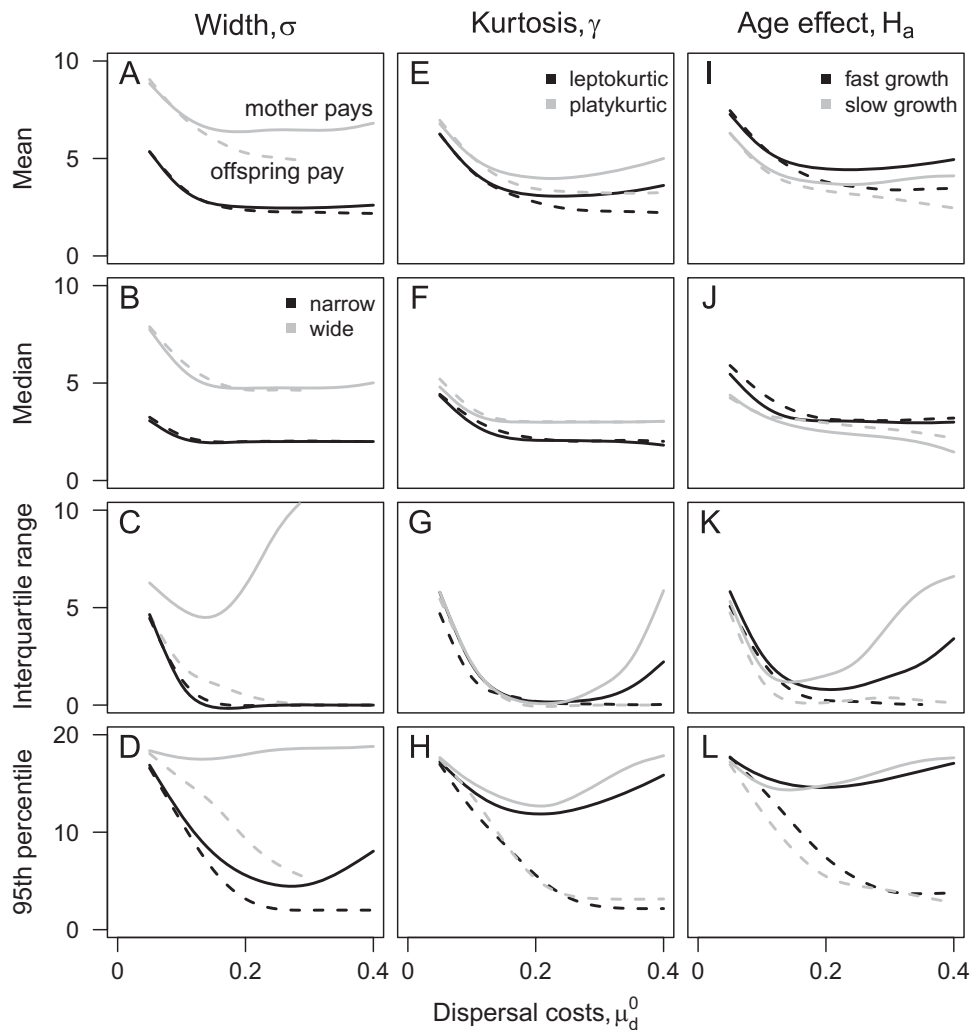
with increasing dispersal costs and allows the emergence of a heavier tail (Fig. 4L; black and grey solid lines intersect). Maternal investment allows to increase the amount of LDD, i.e. tail weight, by increasing the height of the peak at distance zero, i.e. the number of non-dispersers (see also Eq. (2)).

#### 4. Discussion

It has been recognized that in sessile organisms dispersal distance is mainly controlled by the maternal individual (for an analysis of parent-offspring conflict see Starrfelt and Kokko, 2010). It is less well appreciated that the mother may also invest in the dispersal ability of its offspring (Wheelwright and Logan, 2004). Such an investment will necessarily come at a cost, i.e. it will trade off with fecundity or survival. It has been shown in other contexts that trade-offs may shape the evolution of dispersal considerably (Roff, 1994; Burton et al., 2010; Travis et al., 2010; Fronhofer et al., 2011; Travis et al., 2012). We here demonstrate for sessile organisms that trading fecundity for an increased survival of dispersing offspring, i.e. maternal investment, characteristically influences the form of the dispersal kernel. Particularly for high dispersal costs bimodal kernels emerge and, at the same time, the kernels become relatively more fat-tailed. These results prove to be robust against variation in all tested model parameters (Fig. 4 and supporting information). They even hold if the offspring were to pay a part of dispersal costs themselves (supporting information S3).

By relaxing the somewhat arbitrary assumption of a world with discrete habitat patches and modelling inter-individual competition explicitly at the individual level in continuous space through a competition kernel, our results represent an important step towards a better understanding of dispersal in sessile organisms such as plants. Our results from scenarios in which offspring pay distance-dependent dispersal costs (Fig. 2A, B) are in good accordance with findings from Rousset and Gandon (2002). Yet, they show some distinct differences as our model assumes distance-dependent competition (competition kernels), maternal control of dispersal and overlapping generations. Due to decreasing kin competition and increasing (saturating) dispersal costs Rousset and Gandon (2002) also predict unimodal dispersal kernels in two-dimensional landscapes. By explicitly introducing competition for space we can show that the width of the competition kernel ( $\sigma$ ) will determine the location of the kernel's peak. Depending on their specific shape competition kernels may even increase tail weight since competitive interactions are not limited to the size of an arbitrarily defined grid-cell. As described by Starrfelt and Kokko (2010) our kernels are by default more fat-tailed since we assume maternal control of dispersal in comparison to Rousset and Gandon (2002). Finally, when offspring pay dispersal costs our model predicts that all offspring will disperse (Fig. 2A,B; the first distance class has a zero value) because the competition kernel drives all seeds away from the maternal individual. This will not necessarily hold for grid based models, especially if one grid cell may contain more than one individual. Rousset and Gandon (2002) for example, do predict a certain amount of non-dispersers. This effect is especially strong, as the modelled organisms are assumed to be annual in contrast to our model. For the same reasons Starrfelt and Kokko (2010) do not find unimodal kernels.

In scenarios with maternal investment bimodality of the dispersal kernel emerges mainly because of two mechanisms: (i) as the mother pays dispersal costs defined by the dispersal kernel (Eq. (2)) increasing the variance of the kernel through a bimodal distribution with a peak at zero (or at very small distances) allows the mother to decrease the costs while keeping the mean dispersal distance constant or even increasing it through more LDD. Thus, by reducing the dispersal distances of some offspring the mother may achieve LDD for other propagules.



**Fig. 4.** Influence of the shape of the competition kernel. The competition kernel (Fig. 1 and Eq. (4)) is determined by its width (standard deviation  $\sigma$ ; panels A–D), by its kurtosis ( $\gamma$ , panels E–H) and by its height, which is a function of the focal individual's age (half-saturation constant  $H_a$ , panels I–L). As in the previous figure solid lines show results for scenarios with maternal investment ('mother pays') and dashed lines without ('offspring pay'). Black curves always indicate scenarios in which the focal parameter value was halved and grey curves scenarios in which the value was doubled. The characteristic patterns shown before, i.e. bimodal and relatively fat-tailed kernels for maternal investment, are stable. Wide kernels lead to larger dispersal distances (A, B), a more pronounced bimodality (C) and increased tail weight (D). Bimodality emerges also with very narrow competition kernels, yet requires higher dispersal costs. More platykurtic competition kernels tend to underline the described effects, while leptokurtic competition kernels do not lead to a loss of fat tails or bimodality (E–H). Slow growth reduces dispersal distances and underlines the differences between scenarios with and without maternal investment (bimodality, K). Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\sigma = 0.5$  (narrow) or  $\sigma = 2$  (wide),  $\gamma = 1$  (leptokurtic) or  $\gamma = 4$  (platykurtic), and  $H_a = 1.5$  (fast growth) or  $H_a = 6$  (slow growth). The lines are smooth spline regressions (smoothing parameter:  $\lambda = 0.3$ ).

Higher dispersal distances are evolutionarily advantageous because they minimize kin competition (Rousset and Gandon, 2002) an effect known to be especially pronounced for maternal control of dispersal (Hamilton and May, 1977; Starrfelt and Kokko, 2010). (ii) Furthermore, the maternal location has an interesting attribute that makes it attractive for seed deposition. In case of the mother's death it characteristically implies a minimal influence of the nearest neighbors' competition kernels (see Fig. 1, thin black line). Locally this maximizes an individual's survival and non-dispersers will be able to inherit this locally optimal location ('territorial inheritance') after the mother's death (see also Kokko and Ekman, 2002).

It is immediately clear that the latter mechanism will be critically dependent on the assumed width of the first distance class. We therefore tested the impact of increasing the extent of this first class. Our tests show that the bimodality reported here does indeed vanish for coarse grids but is stable for a width of the first distance class ( $d_1$ ) of up to  $0 \leq d \leq 0.2$  (see also Fig. 2). This result underlines the possible artifacts resulting from grid-based models in general (see also Chipperfield et al., 2011).

The two mechanisms discussed above also explain the influence of the age-specific component of the competition kernel (Fig. 4) and of fecundity (see supporting information S2). Increased local competition through fast growth leads to a reduction of kernel bimodality in scenarios with maternal investment. Although there is an advantage for mothers keeping a fraction of offspring close by for territorial inheritance fast growth leads to an important increase in local competition between the mother and her non-dispersing offspring and between these. This leads to a reduction of the peak at distance zero, i.e. the number of non-dispersers. The same effect will emerge from increased numbers of offspring. As the kernel costs resulting from the formation of a relatively fat tail are offset by the production of 'cheaper' non-dispersers, reducing the latter will lead to a reduction of tail weight.

Due to asymmetric competition between the mother and the offspring a majority of non-dispersers may actually die. This of course begs the question why mothers produce these offspring in the first place. If this was just a strategy to spare resources for the production of more expensive long-distance dispersers and these 'cheap' propagules were thus only produced to reduce the

costs of offspring production, mothers could as well simply reduce the number of offspring produced and put all resources into long-distance dispersers. In order to explore this question we ran additional numerical analyses including evolvable fecundities and a trade-off between fecundity and baseline mortality (supporting information S6 and S7). In all these model runs, the bimodality was evolutionarily stable (supporting information S6) which highlights the value of 'territorial inheritance' (see [Dytham and Travis, 2006](#), for an analysis of the concurrent evolution of longevity and dispersal distance).

Interestingly the occurrence of a bimodal kernel that generates non-dispersers and long-distance dispersers parallels the co-occurrence of philopatrics and dispersers found in models of actively moving organisms that include a trade-off between fertility and dispersal ability ([Roff, 1994](#); [Fronhofer et al., 2011](#)). Yet, as these models assume offspring control of dispersal and consider emigration rates only, the underlying mechanisms are different (see also below). In recent work that incorporates such a trade-off into an explicit movement model [Travis et al. \(2012\)](#) show that emigration rates increase for high levels of investment in movement. Although we also find more LDD in our model, emigration rates actually decrease which is due to the kernel's bimodality.

In general, maternal investment, i.e. trading fecundity for an increased survival of dispersing offspring, is highly advantageous. It allows the persistence of stable populations despite low fecundities, high mortalities and high competition, conditions that otherwise lead to global extinctions. This can be seen, e.g., in the supporting information figure S2 A–D: for low fecundities and if the offspring pay distance dependent dispersal costs populations are not viable for dispersal costs  $\mu_d^0 > 0.3$ . This is not the case in scenarios with maternal investment. Additional numerical analyses show that maternal investment allows populations to survive dispersal costs over 0.8 (not shown). Simulation experiments also show that the 'mother pays' strategy is evolutionarily stable (supporting information S4).

To summarize so far and put our results in a broader context, if the offspring control dispersal previous work has shown that the evolutionarily stable kernel must guarantee equal fitness expectations for all offspring ([Rousset and Gandon, 2002](#)). This logic does not apply if dispersal is controlled maternally as we assume in this study: the parent-offspring conflict (discussed in the context of dispersal distances in [Starrfelt and Kokko, 2010](#)) leads to larger dispersal distances, as the mother maximizes its own inclusive fitness expectations by reducing kin competition. If the offspring pay dispersal costs, these costs are the only mechanism that restrain dispersal distance and counteract the effect of (kin) competition which drives seeds away from the mother. This cost-benefit calculation is fundamentally changed if the mother also pays dispersal costs. Increasing dispersal costs lead to selection for non-dispersers in spite of strong competition with the maternal individual, as this allows the mother to reduce its investment in propagule dispersal ability, which in turn allows for more LDD. Simultaneously, selection seems to favor a reduction in longevity for an increase in fecundity. Ultimately, this may lead to highly fertile, short lived organisms with strongly bimodal dispersal kernels (see supporting information S6 and S7). Note that our results are robust with regard to the position of the paternal individual (see supporting information figure S1 for global random mating).

#### 4.1. Examples

Our model is applicable to sessile organisms such as plants. Most plants will show maternal investment, at least to some degree, since fruit and seed production is obviously maternally regulated. The bimodal dispersal kernel which we predict can be realized for example by seed polymorphisms, a phenomenon that has been frequently

observed ([Imbert, 2002](#)). The Asteraceae *Heterotheca latifolia*, for example, shows a dimorphism in achene structure: while disc achenes, which have a pappus, are wind dispersed and responsible for LDD ray achenes are not ([Venable and Levin, 1985](#)). This polymorphic seed structure will lead to bimodality in the dispersal kernel and increased tail weight ([van Mólken et al., 2005](#); [Brändel, 2007](#)). The same effect can be achieved by polychory, i.e. the use of more than one seed dispersal agent ([Berg, 1966](#); [Jordano et al., 2007](#); [Russo et al., 2006](#)). For example in *Prunus mahaleb* small birds are responsible for short distance dispersal while fruits eaten by mammals and larger birds are dispersed over long distances ([Jordano et al., 2007](#)). Similar 'kernel mixing' strategies have also been reported in passively dispersing animals (e.g. [Fronhofer et al., 2013](#)). In addition, our results are in good accordance with the increasing evidence that multiple seed size strategies, directly leading to different dispersal distances, may generally be due to life-history trade-offs (competition-colonization or stress tolerance-fecundity trade-offs, see e.g. [Jakobsson and Eriksson, 2003](#); [Lönnberg and Eriksson, 2013](#)). Of course, in purely wind-dispersed plants with monomorphic seeds such as modelled by [Travis et al. \(2010\)](#) trade-offs may also occur between plant height which influences dispersal distance and seed production. Such trade-offs may then lead to the evolution of different plant heights depending on habitat availability or local extinctions, for example (for the effect of local extinctions on the evolution of dispersal kernels see [Fronhofer et al., 2014](#)).

#### 4.2. Simplifications

As in any tractable model we include some simplifying assumptions, a number of which we have already dealt with throughout this paper. A central simplification we have made is that dispersal strategies, i.e., the dispersal kernel, are not age-dependent, although we assume overlapping generations. Maternal age-dependent dispersal has been analyzed by [Ronce et al. \(1998\)](#) who provide theoretical and empirical evidence that such a strategy is evolutionarily advantageous, for both maternal and offspring control of dispersal. As we have discussed above the emerging bimodal dispersal kernel is a result of cost optimization in order to allow LDD and at the same time insures territorial inheritance. Yet, these two aspects are advantageous respectively early and late in the life of an individual. We hypothesize that age-dependent kernels would be fat-tailed in early life stages and more biased towards short-distance dispersal and the production of non-dispersing offspring later on in order to reduce (kin) competition but still allow territorial inheritance.

Obviously, the uniformity and stability of the landscape we assume here is a further simplification. Although space is continuous in our model, it is homogeneous and shows no habitat structure or turnover. As [Hovestadt et al. \(2001\)](#) predict fat-tailed dispersal kernels to emerge in autocorrelated landscapes, we are confident that the introduction of spatial structure would not alter our results fundamentally (for a detailed treatment of the influence of habitat structure on dispersal distance, see [North et al., 2011](#)). Of course, patch size would interact with the competition kernel and influence the evolving mean dispersal distance and the location of the dispersal kernel's maximum or second peak for bimodal kernels. Yet, as the introduction of suitable and non-suitable habitat basically leads to an increase in dispersal costs we hypothesize that spatial structure would only underline our results for both scenarios. Especially in scenarios with maternal investment the bimodality of the dispersal kernel should be more pronounced, provided that patches are large enough to support more than one individual. A bimodal kernel is highly advantageous in fragmented landscapes with patch turnover as well, since the fat tail and resulting LDD allows individuals to colonize distant and empty patches. At the same time the non- and short distance-dispersers



emerging from the same kernel in the next generation guarantee a successful and sustained establishment (North et al., 2011).

#### 4.3. Conclusions

Although the concept of a dispersal kernel is not new, only little work has been done on the evolution of the shape of dispersal kernels. In contrast to previous work (Hovestadt et al., 2001; Rousset and Gandon, 2002; Starrfelt and Kokko, 2010) we have concentrated on two important aspects that have received little attention in this context up to now: (i) the effects of individual competition kernels in continuous space and (ii) maternal investment. We predict the emergence of long-distance dispersal and bimodal dispersal kernels for sessile organism with overlapping generations in environments with costly dispersal.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2014.10.024>.

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# 1 Supporting Information

2 Fronhofer, E.A., Poethke, H.J. and Dieckmann, U.: Evolution of dispersal distance: ma-  
3 ternal investment leads to bimodal dispersal kernels

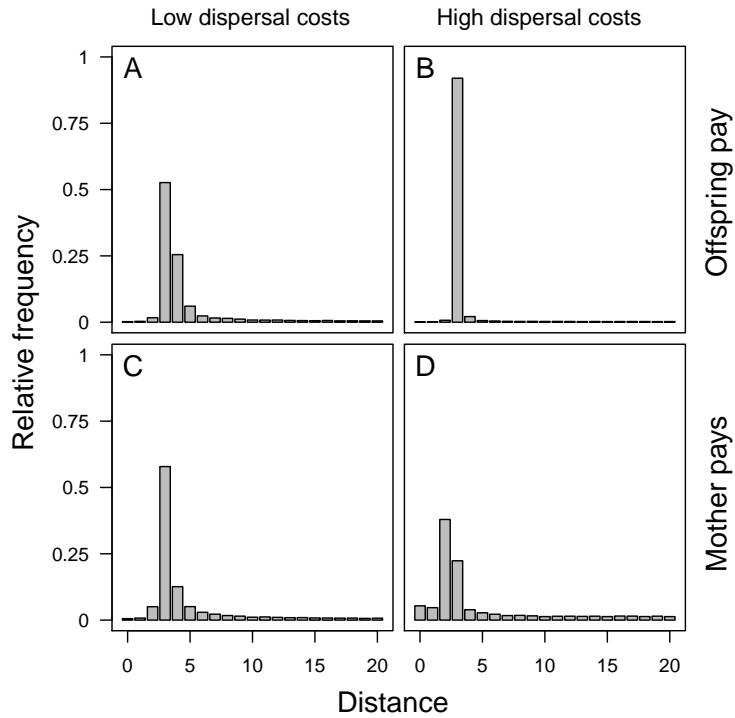


Figure S1: Maternal investment and the evolution of dispersal kernels under global random mating. All four panels show evolutionarily stable dispersal kernels (distance pdfs). These results are analogous to figure 2, except that mating occurs with a randomly chosen partner independently of distance and not with the nearest neighbour. The upper row (A, B) depicts the influence of dispersal costs without maternal investment, i.e. when offspring pay distance-dependent dispersal costs according to equation 1. The lower row (C, D) shows kernels for scenarios with maternal investment, i.e. the mother pays kernel-dependent dispersal costs (equation 2) and reduces her fecundity in order to maximize offspring survival during dispersal (equation 3). Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.1$  (left panels; A, C) or  $\mu_d^0 = 0.4$  (right panels; B, D).

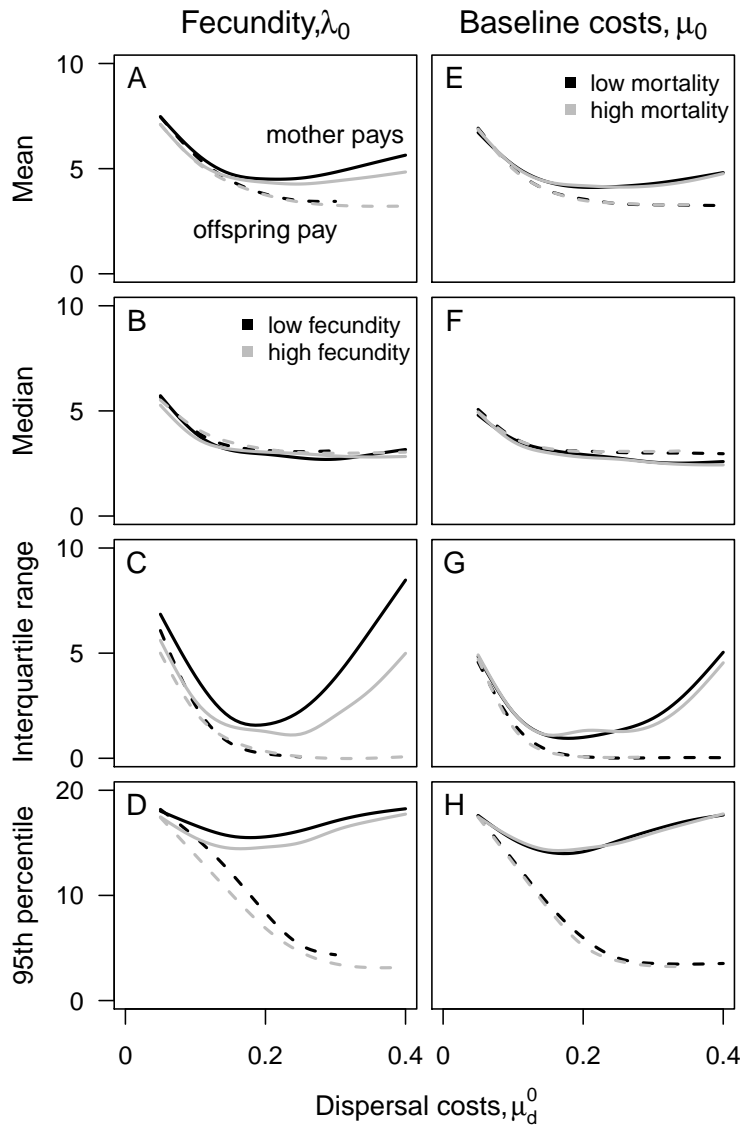


Figure S2: Influence of fecundity and mortality. Solid lines show results for scenarios with maternal investment ('mother pays') and dashed lines without ('offspring pay'). Black curves always indicate scenarios in which the focal parameter value was halved and grey curves scenarios in which the value was doubled. Low fecundities ( $\lambda_0$ ) underline the effects described above (A–D), but higher fecundities do not destroy the patterns, i.e., relatively fat tails and bimodality for maternal investment still arise at sufficiently high dispersal costs. Density independent baseline mortality ( $\mu_0$ ; E–H) does not influence our results in a quantitatively relevant way. Parameters:  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ ,  $\lambda_0 = 2$  (low fecundity) or  $\lambda_0 = 8$  (high fecundity), and  $\mu_0 = 0.05$  (low mortality) or  $\mu_0 = 0.2$  (high mortality). The lines are smooth spline regressions (smoothing parameter:  $\lambda = 0.3$ ).

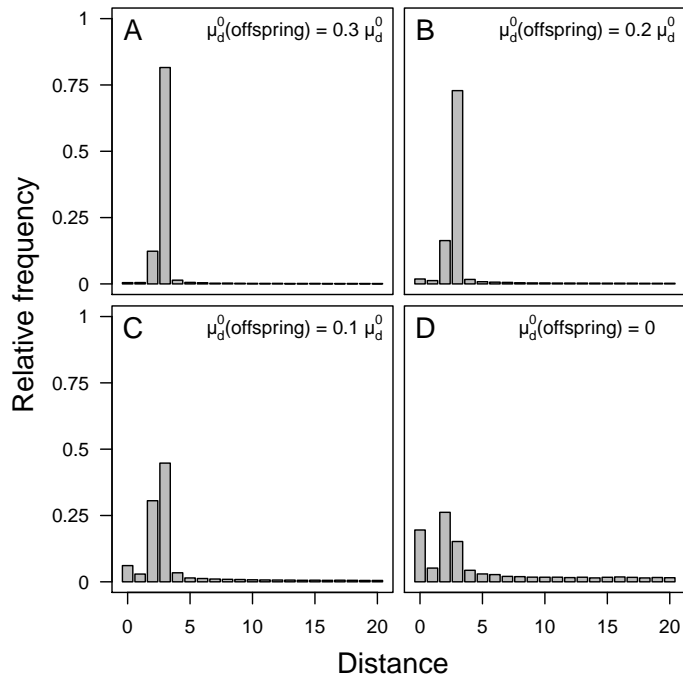


Figure S3: Allocation of dispersal costs to mother vs. offspring and the evolution of dispersal kernels. All four panels show evolutionarily stable dispersal kernels (distance pdfs) for scenarios in which dispersal costs are allocated proportionally to both, mothers and offspring. Depending on the allocation parameter a proportion of the total distance dependent dispersal costs ( $\mu_d^0$ ) is paid by the mother and the remaining costs are paid by the offspring. These results show that if both, mother and offspring, have to pay dispersal costs our results hold up in principle. Of course, the pattern is sensitive as total costs are divided. Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.4$ .

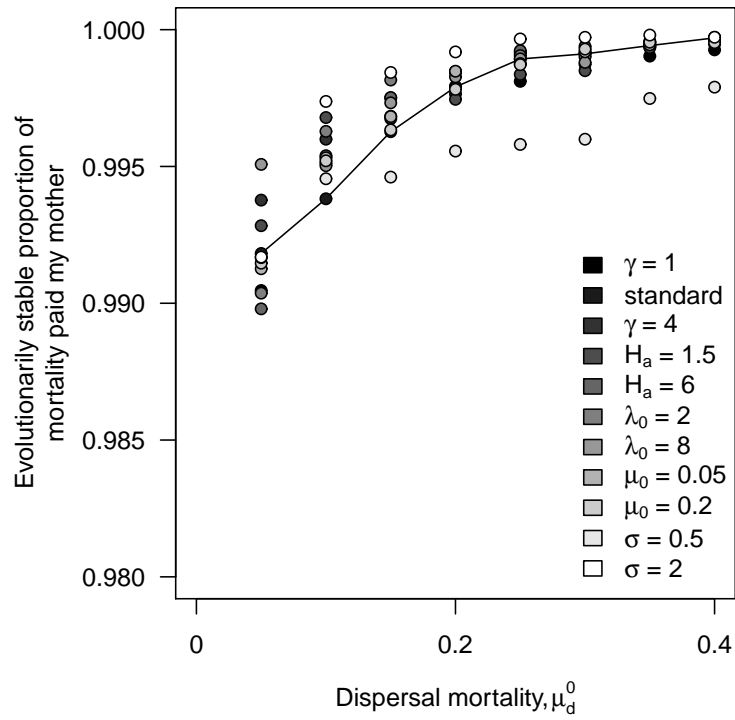


Figure S4: Evolutionarily stable allocation of dispersal costs to mother vs. offspring. We here allowed the allocation of costs to be itself an evolvable trait: depending on this trait a proportion of the distance dependent dispersal costs ( $\mu_d^0$ ) is paid by the mother and the remaining costs are paid by the offspring. For all tested parameter combinations (table 1) no intermediate cost allocation strategy evolved and the evolutionarily stable strategy was full maternal investment, i.e. ‘mother pays’. Note the scale of the y-axis. The line corresponds to the our standard parameter combination.

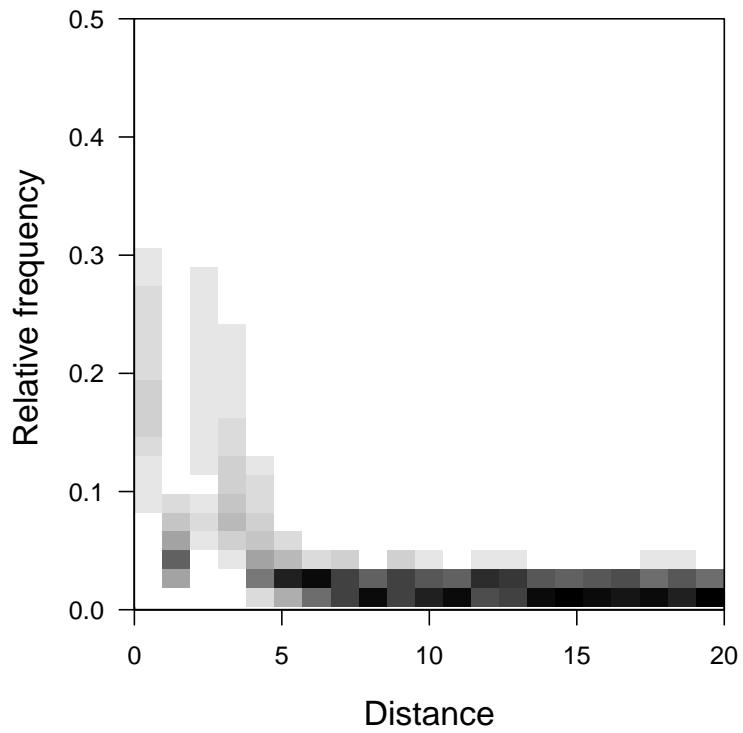


Figure S5: Evolutionarily stable dispersal kernel as a 2D histogram. This figure corresponds to figure 2 D and shows the strategies of all individuals across all 25 replicate simulation runs. Clearly, the bimodality occurs at the individual kernel level and is not a result of a mixed strategy at population level. Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.4$ .

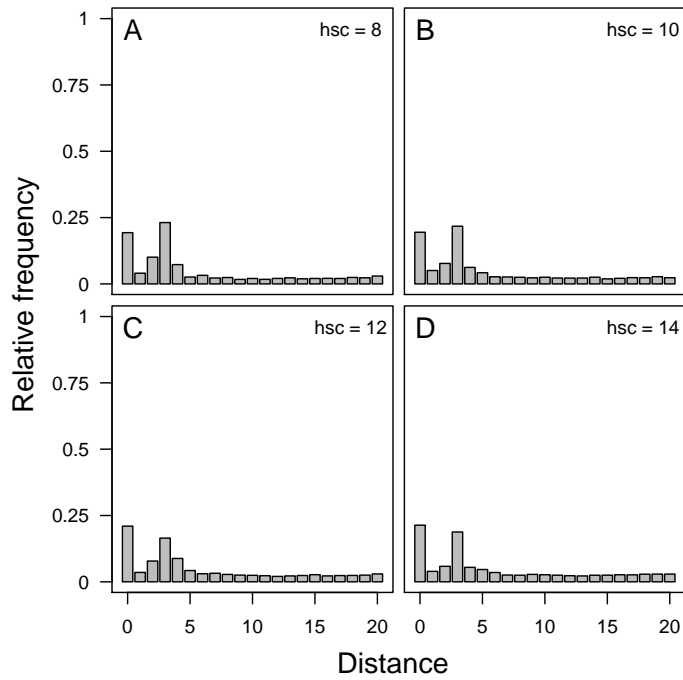


Figure S6: Maternal investment, baseline mortality - fertility trade-off, and the evolution of dispersal kernels. All four panels show evolutionarily stable dispersal kernels (distance pdfs) for scenarios with maternal investment, a trade-off between baseline mortality and fecundity and evolving fecundities. The trade-off function is saturating and follows the general form  $\mu_0 = \lambda_0 / (\lambda_0 + hsc)$  (see figure S6). Clearly, bimodality is not affected by the inclusion of this additional trade-off. Parameters:  $\lambda_0 = \text{evolving}$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.4$ .



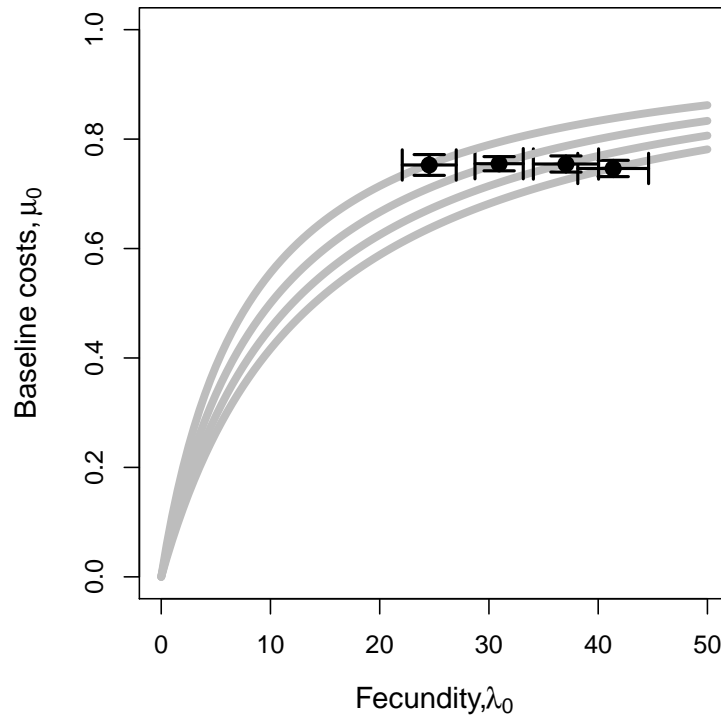


Figure S7: Maternal investment, baseline mortality - fertility trade-off, and the evolution of dispersal kernels. The figure shows the evolutionarily stable fertility (mean and standard deviation) and the corresponding baseline mortality for scenarios with maternal investment and a trade-off between baseline mortality and fecundity. The grey lines depict a sample of tested trade-off functions (from top to bottom:  $hsc = 8, 10, 12, 14$ ). Here, the trade-off function is saturating and follows the general form  $\mu_0 = \lambda_0 / (\lambda_0 + hsc)$ . Similar results were obtained for linear and concave functions. Such trade-offs lead to highly fertile annual organisms with strongly bimodal dispersal kernels (figure S5). Parameters:  $\lambda_0 = \text{evolving}$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.4$ .

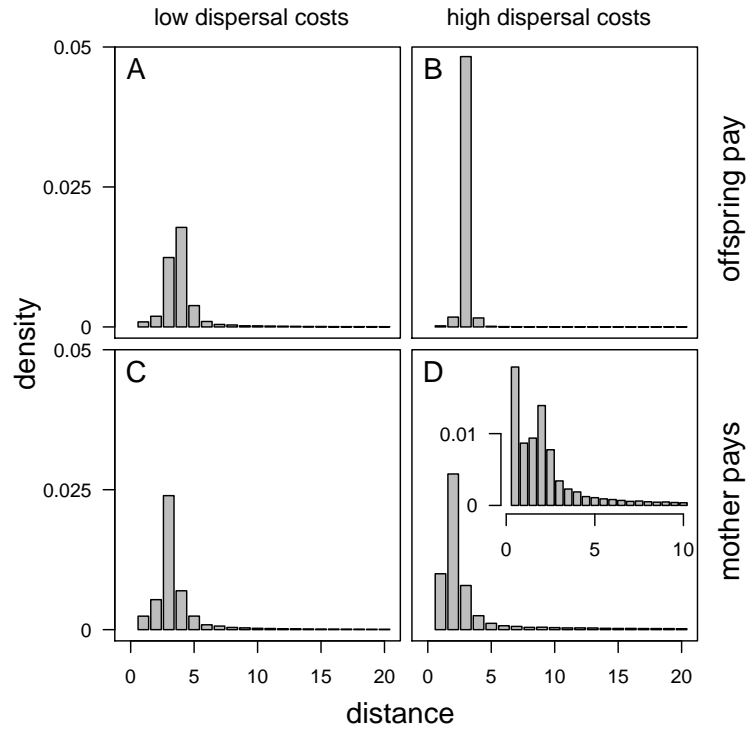


Figure S8: Maternal investment and the evolution of dispersal kernels. This figure shows the same results as figure 2, yet kernels are represented as density pdfs. As non-zero relative frequencies of dispersal to the zero distance class (first bar; see figure 2) lead to infinite values in the density pdf we omitted these values here. The bimodality and relative increase in tail weight due to maternal investment described in figure 2 can also be observed in the density pdf (inset in panel D; distance class extent of 0.5 instead of the default of 1). Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.1$  (left panels; A, C) or  $\mu_d^0 = 0.4$  (right panels; B, D).