

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

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## Abstract

1

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

## 16 Introduction

17 Understanding and eventually predicting the distribution of species in space and time has never been  
18 more important. Within the boundaries of local adaptation a species' range is mainly influenced by its  
19 dispersal abilities (Kokko & López-Sepulcre, 2006). Consequently there are numerous empirical and even  
20 more theoretical studies on dispersal of plants and animals (Clobert *et al.*, 2012), but so far, particularly  
21 theoretical studies on dispersal have mainly focused on the emigration propensity of individuals, while the  
22 dispersal process itself and the question how far to disperse has been mostly ignored or tackled with rather  
23 arbitrary assumptions like nearest neighbour (e.g. Travis *et al.*, 1999; Gros *et al.*, 2006) or global dispersal  
24 (e.g. Poethke & Hovestadt, 2002). However, the growing awareness of the enormous influence of dispersal  
25 distances on colonization and range expansion particularly in plants (Nichols & Hewitt, 1994; Nathan  
26 *et al.*, 2002; Bohrer *et al.*, 2005; Nathan, 2006; Alsos *et al.*, 2007) has inspired a more thorough analysis of  
27 so-called dispersal kernels — the statistical distribution of propagules in terms of distances travelled from  
28 their origin (Cousens *et al.*, 2008; Hovestadt *et al.*, 2012). The specific form of such kernels defines not  
29 only the mean dispersal distance, but also the occurrence of potentially important but rare long-distance  
30 dispersal events (LDD; Kot *et al.*, 1996; Muller-Landau *et al.*, 2003). 'Fat-tailed' distributions, which  
31 imply a relatively large proportion of LDD, increase the velocity of species invasions (Kot *et al.*, 1996;  
32 Caswell *et al.*, 2003), their ability to cope with habitat fragmentation (Dewhurst & Lutscher, 2009), and  
33 may influence biogeographic patterns of species diversity (Chave *et al.*, 2002; Nathan, 2006).

34 An additional challenge arises from the term 'dispersal kernel' not always being clearly defined. A  
35 kernel may be described by two distinctly different probability-density functions (pdfs): (i) the density  
36 pdf, which describes the density of propagules to be expected at a certain distance, and (ii) the distance  
37 pdf, which describes the distribution of distances the propagules are dispersed to (see also Cousens *et al.*,  
38 2008; Hovestadt *et al.*, 2012). While both definitions are correct and kernels can be expressed either way,  
39 their shapes will systematically differ. For example, if one considers a uniform distribution of propagules  
40 per area up to a certain maximal dispersal distance, the density pdf will look like a cylinder, while the  
41 distance pdf will be a linearly increasing function of distance up to the maximal dispersal distance. This  
42 is simply due to the fact that in two dimensions the area of a circle increases quadratically with its radius,  
43 so the area of a thin ring at the circle's perimeter increases linearly with its radius. Thus, if the propagule  
44 density is to be constant within each ring independent of its radius, proportionally more propagules have  
45 to be dispersed to larger distances, so as to yield the same propagule density for larger rings. Throughout  
46 this manuscript, we express dispersal kernels in terms of their distance pdf.

47 In spite of the immense relevance of the specific form of the dispersal kernel, it is still unclear how an  
48 optimal or evolutionarily stable kernel should look like. This question has been addressed for the first time

49 by Hovestadt *et al.* (2001), who found that fat-tailed dispersal kernels evolve in autocorrelated landscapes  
50 (and at sufficiently fine scales, all landscapes are autocorrelated). While a certain fraction of propagules  
51 will disperse to the immediate surroundings of the parent, a significant fraction of propagules will exhibit  
52 long-distance dispersal: the latter propagules disperse more or less uniformly over the landscape, which  
53 minimizes kin competition (Hamilton & May, 1977; Rousset & Gandon, 2002). The shape of the dispersal  
54 kernel can thus be understood as the result of two opposing selection pressures: kin competition would be  
55 minimized by a completely uniform distribution of propagules, while distance-dependent dispersal costs  
56 (for a review, see Bonte *et al.*, 2012) select against long-distance dispersal.

57 While Hovestadt *et al.* (2001) include dispersal costs only implicitly, via an assumption of increasingly  
58 unsuitable habitat Rousset & Gandon (2002) explicitly analysed the effect of distance-dependent dispersal  
59 costs. They predict unimodal dispersal kernels (in terms of the distance pdf) for all scenarios with  
60 costs monotonically increasing with dispersal distance. Like most studies on dispersal evolution Rousset  
61 & Gandon (2002) assume that dispersal is under the control of the dispersing individual. Yet, this  
62 assumption is rather unlikely to be completely true for passively dispersing propagules like seeds. Thus,  
63 Starrfelt & Kokko (2010) have studied the evolution of dispersal distance and kernel shapes in the context  
64 of parent-offspring conflict. They could show that maternal control of dispersal generally leads to longer  
65 dispersal distances and even to fat-tailed kernels.

66 While all these earlier studies represent important steps towards a better understanding of the evo-  
67 lution of the shapes of dispersal kernels, two fundamental issues known to heavily influence dispersal  
68 evolution have not yet been taken into account: (i) effects of the overall strength, and gradual attenua-  
69 tion with distance, of competitive interactions have not been considered, and (ii) effects of trade-offs in  
70 parental investment into offspring dispersal have not been investigated. Firstly, as Berger *et al.* (2008)  
71 point out, competition is a process that fundamentally shapes the spatial patterns found in plant com-  
72 munities and that needs to be modeled at the individual level (see e.g. Law *et al.*, 2003; Travis *et al.*,  
73 2010; North *et al.*, 2011), and not only at the population level. A large number of models in dispersal  
74 ecology are grid-based (e.g. Murrell *et al.*, 2002; Gros *et al.*, 2006; Bonte *et al.*, 2010), which implies either  
75 that competition acts at the local population level, or — if only one individual is allowed per grid cell  
76 — that the assumed competition kernel has a quadratic base, which is a somewhat artificial assumption.  
77 Secondly, if one concedes that in passive dispersers the dispersal process, more specifically the dispersal  
78 distance, is centrally influenced by the parent organism (‘maternal control’ as in Starrfelt & Kokko 2010)  
79 it is also very likely that parents will invest in the dispersal abilities of their offspring (for empirical  
80 evidence see Wheelwright & Logan, 2004). It has been shown theoretically and empirically (e.g. Roff,  
81 1994; Fronhofer *et al.*, 2011; Burton *et al.*, 2010; Travis *et al.*, 2010, 2012) that life-history trade-offs,  
82 e.g., between reproduction and dispersal ability, may deeply influence the evolution of dispersal, in a way

83 that may lead, for example, to polymorphisms in which low-dispersal and high-dispersal morphs coexist.  
84 In the context of sessile organisms with passive dispersal, such trade-offs are inter-generational and are  
85 more appropriately described in terms of maternal investments that may offset an offspring's dispersal  
86 costs. Especially in plants, in which seeds are surrounded by maternal tissue and may depend on these  
87 structures for dispersal, it is sensible to include this aspect and to analyze the consequences of such  
88 maternal investment.

89 Therefore, we here present an individual-based model of a population of sessile organisms, such as  
90 trees or corals, and investigate the evolution of the shapes of dispersal kernels. In contrast to the great  
91 majority of existing models (e.g. Murrell *et al.*, 2002; Gros *et al.*, 2006; Bonte *et al.*, 2010; North *et al.*,  
92 2011), we do not *a priori* assume any specific kernel shape. Instead, we derive evolutionarily optimal  
93 kernel shapes under the assumption that long-term evolution can find ways to realize them. We explicitly  
94 account for three different selection pressures of relevance for the evolution of the shape of dispersal  
95 kernels: distance-dependent competition (e.g., Roughgarden, 1974; Law *et al.*, 2003; Travis *et al.*, 2010;  
96 North *et al.*, 2011), distance-dependent dispersal costs (for a review, see Bonte *et al.*, 2012), and maternal  
97 investment reducing the dispersal costs experienced by dispersing offspring.

## 98 The model

99 In our model, each individual ( $i = 1, \dots, N$ ) is characterized by its location  $(x_i, y_i)$  and its dispersal kernel  
100 ( $P_i$ ). Individuals are located in a two-dimensional spatially continuous and homogeneous habitat, with  
101  $0 \leq x_i, y_i \leq 100$  and periodic boundary conditions. Time is discrete and generations are overlapping.

## 102 Dispersal kernels

103 We define dispersal kernels as probability distributions ( $P(d)$ ) of reaching a distance ( $d$ ) after a dispersal  
104 event, i.e., we use a distance pdf. Since we do not *a priori* restrict attention to a specific functional  
105 relationship between  $P$  and  $d$ , the dispersal kernels in our model are implemented as function-valued  
106 traits (Dieckmann *et al.*, 2006). As is common in studies of function-valued traits, we approximate the  
107 theoretically infinite-dimensional trait by a sufficiently large, but finite, number of values. Specifically,  
108 we use  $n = 21$  values to describe the probabilities of reaching a distance class ( $d_k$ ,  $k = 1, \dots, n$ , with  $d_1$   
109 corresponding to  $d = 0$ ,  $d_2$  corresponding to  $0 < d \leq 1$ ,  $d_3$  corresponding to  $1 < d \leq 2$ , ..., and with  
110  $d_{21}$  corresponding to  $19 < d \leq 20$ ). All values  $d_k$  are positive and are normalized so as to sum up to 1,  
111  $\sum_{k=1}^n P(d_k) = 1$  (see also Hovestadt *et al.*, 2001; Starrfelt & Kokko, 2010).

112 To ensure that the chosen trait discretization does not unduly influence our results, we carried out  
113 additional numerical analyses with up to  $n = 31$  distance classes. We also analyzed the effect of increasing

114 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  
115  $0 \leq d \leq 0.2$ ). These robustness checks are discussed in detail below; here we only mention that our  
116 results remained essentially unchanged.

## 117 **Reproduction**

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

## 123 **Inheritance**

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

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

## 137 **Dispersal**

138 As we investigate the evolution of the dispersal kernel of sessile organisms with passive dispersal, we  
139 assume maternal control of dispersal (see also North *et al.*, 2011). This means that the mother's genotype  
140 defines the dispersal distance of the offspring. As Hamilton & May (1977) note optimal dispersal distances  
141 may be different depending on whether one maximizes the inclusive fitness of the mother or of the  
142 offspring. Due to costs of dispersal applying directly to the offspring, dispersal distances under offspring  
143 control are often reduced. This has been analyzed in detail by Starrfelt & Kokko (2010). We have run

144 additional numerical analyses with offspring control and found that the results corresponded well to their  
145 results.

146 The dispersal distance of an offspring is determined by randomly drawing a distance class ( $d_k$ ) ac-  
147 cording to the maternal dispersal kernel ( $P(d_k)$ ). The realized dispersal distance is drawn randomly with  
148 a uniform distribution from this interval, i.e., if  $d_1$  is drawn the dispersal distance ( $d$ ) is always zero, if  
149  $d_2$  is drawn the dispersal distance is between 0 and 1 ( $0 < d \leq 0.1$ ) and so forth.

## 150 Dispersal costs and maternal investment

151 As we assume a constant per step mortality ( $\mu_d^0$ ) the probability of dying while dispersing over a given  
152 distance ( $\delta$ ) follows an exponential function (figure 1)

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

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

161 Dispersal costs may be offset — at least to some extent — by maternal investment which increases the  
162 dispersal ability of propagules. Such a trade-off implies that, although investment of resources increases  
163 one component of fitness, another component of fitness is reduced (Roff & Fairbairn, 2007). Very often  
164 an increase in dispersal ability is correlated with a decrease in fertility (Zera & Denno, 1997; Tanaka &  
165 Suzuki, 1998; Roff, 2002; Roff *et al.*, 2002).

166 For simplicity we will assume two extreme scenarios: (i) either the offspring carry all costs as described  
167 above (equation 1; scenario ‘offspring pay’) or (ii) the costs are completely covered by maternal investment  
168 (scenario ‘mother pays’). To keep both scenarios comparable we determine the maternally covered,  
169 kernel-dependent, costs by summing up the distance-dependent costs over the entire kernel ( $P(d_k)$ ) for  
170 all possible distance classes ( $d_k$ ),

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

171 Costs trade-off with fecundity (see also Burton *et al.*, 2010; Fronhofer *et al.*, 2011) and the mean number

172 of offspring is then calculated as

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

173 with  $\lambda_0 = 4$  as our default choice.

174 Note that in order to analyse the influence of relaxing this strong assumption of either ‘mother pays’  
175 or ‘offspring pays’ we ran two classes of additional numerical analyses. Firstly, we show that if both,  
176 mother and offspring, have to pay dispersal costs our results hold up to a considerable amount of costs  
177 paid by both (supporting information S3). Secondly, we allowed the allocation of costs to be itself an  
178 evolvable trait: depending on this trait a proportion of the distance dependent dispersal costs ( $\mu_d^0$ ) is paid  
179 by the mother according to equation 2 and the remaining costs are paid by the offspring (equation 1).  
180 For all tested parameter combinations (table 1) no intermediate cost allocation strategy evolved and the  
181 evolutionarily stable strategy was full maternal investment, i.e. ‘mother pays’ (see supporting information  
182 S4).

## 183 **Competition and mortality**

184 No matter whether competition is for space, light or nutrients it will always depend on inter-individual  
185 distances. In addition and in contrast to previous models that assume annual organisms with non-  
186 overlapping generations (e.g. Travis *et al.*, 2010; North *et al.*, 2011) we include age-dependence since  
187 competition will be asymmetric between established trees and seedlings, for example. In our model,  
188 competition acts by increasing mortality, and not by decreasing fertility (figure 1). This allows us to  
189 derive a density-dependent individual mortality term, i.e. the probability of dying in the present time  
190 step ( $\mu_i$ ). For the form of this competition kernel — often termed zone or sphere of influence (for  
191 a review of modeling approaches, see Berger *et al.*, 2008) — we assume a general and very flexible  
192 functional relationship (analyzed in detail by Roughgarden, 1974). This approach is similar to the sphere  
193 of influence model presented by Schiffrers *et al.* (2011). The effect of an individual  $j$  on the focal individual  
194  $i$  is calculated as

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

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



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

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

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

208 Please see figure 1 for a summary of all mortality components. This figure includes the effects of all  
209 individuals in a landscape as in equation 5 and additionally illustrates the dominant effect of the focal  
210 individual.

## 211 Numerical analyses

212 All analyses were run in a world of 100 x 100 distance units with periodic boundary conditions. Depending  
213 on parameter combinations populations sizes varied roughly between 400 and over 7000 individuals.  
214 Computing time was set to  $t_{\max} = 10,000$  time steps, a time span that allowed all model runs to reach  
215 equilibrium. The results shown below are means over 25 replicates. Please see table 1 for a summary of  
216 relevant parameters and tested values.

## 217 Results

### 218 Evolution of dispersal kernels

219 In all scenarios without maternal investment, i.e. when the offspring pay distance-dependent dispersal  
220 costs according to equation 1, we find that the evolutionarily stable dispersal kernel is unimodal (fig-  
221 ure 2 A). This results from the interaction between the competition kernel, competition with related  
222 dispersers and dispersal costs (see figure 1). Increasing dispersal costs lead to narrower, more peaked and  
223 less fat-tailed kernels (figure 2 B). This is due to an increase in the slope of the dispersal cost function  
224 (figure 1).

### 225 Maternal investment leads to bimodal kernels

226 In general, maternal investment increases the occurrence of LDD, i.e. the weight of the kernel's tail (fig-  
227 ure 2). Interestingly, maternal investment inverts the effect of dispersal costs on long-distance dispersal:

228 here increasing dispersal costs lead to an increase in tail weight (figure 2 D). In addition, the evolution-  
229 arily stable dispersal kernel for high dispersal costs is bimodal (figure 2 D) with an important proportion  
230 of propagules remaining very close to the maternal individual and a mass of offspring showing LDD. The  
231 inset in figure 2 D shows the same numerical analysis for an increased resolution of the dispersal kernel  
232 (distance class extent of 0.5 instead of the default of 1). Note that the bimodality we describe here occurs  
233 at the individual level and is not the result of a mixed strategy with coexisting short- and long-distance  
234 dispersers (supporting information S4).

## 235 **Dispersal costs**

236 A more detailed analysis of the influence of dispersal costs shows that, as one would assume, the mean  
237 dispersal distance decreases with costs in the ‘offspring pay’ scenario (figure 3 A). Yet, with maternal  
238 investment (‘mother pays’) the relationship becomes u-shaped, i.e. higher dispersal costs favour higher  
239 mean dispersal distances (figure 3 A). Clearly, this is due to the asymmetry and tail weight of the kernels  
240 (figure 2) since the median dispersal distance decreases monotonically with dispersal costs (figure 3 B).  
241 The median reaches a steady value which is defined by the width of the competition kernel (see also  
242 figure 4). The scenario assumed, i.e. distance costs paid by the offspring (‘offspring pay’) vs. kernel costs  
243 paid by the mother (‘mother pays’), does not influence the median dispersal distance.

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

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

## 252 **Shape of the competition kernel**

253 The qualitative results presented above, i.e. the emergence of fat-tailed and bimodal kernels in scenarios  
254 with maternal investment, are robust against variation in all model parameters (figure 4 and supporting  
255 information S1). Not surprisingly, the width of the competition kernel influences the mean and the  
256 median of the dispersal kernel, i.e. the location of the peak (figure 4 A, B). Wider competition kernels,  
257 i.e., higher values of the standard deviation ( $\sigma$ ), lead to bimodal dispersal kernels at lower dispersal costs  
258 in the ‘mother pays’ scenario (figure 4 C, D). The pattern is not lost for narrower competition kernels,

259 yet requires higher dispersal costs to emerge ( $\mu_d^0 > 0.5$ ; not shown).

260 The kurtosis of the competition kernel ( $\gamma$ ) has only very slight effects. More leptokurtic shapes  
261 lead to slightly smaller dispersal distances (figure 4 E, F) because the costs inflicted by competition  
262 decrease at a faster rate at small distances. As a consequence more platykurtic competition kernels lead  
263 to bimodality in ‘mother pays’ scenarios at lower dispersal costs (figure 4 G) and to more pronounced fat  
264 tails (figure 4 H).

265 The shape, especially the height of the competition kernel, also depends on the focal individual’s  
266 age (equation 4). We find that the slower an individual’s competitive ability increases (‘slow growth’ in  
267 figure 4; larger values of the half-saturation constant  $H_a$ ) the smaller dispersal distances become (figure 4 I,  
268 J). Under such conditions the usual pattern of higher dispersal distances in scenarios with maternal  
269 investment is inverted (figure 4 J) which is due to a more pronounced bimodality (figure 4 K) with a  
270 higher peak at distance zero. This is primarily due to the lower competitive ability of a focal maternal  
271 individual. In turn, this pattern interacts with increasing dispersal costs and allows the emergence of a  
272 heavier tail (figure 4 L; black and grey solid lines intersect). Maternal investment allows to increase the  
273 amount of LDD, i.e. tail weight, by increasing the height of the peak at distance zero, i.e. the number of  
274 non-dispersers (see also equation 2).

## 275 Discussion

276 It has been recognized that in sessile organisms dispersal distance is mainly controlled by the maternal  
277 individual (see Starrfelt & Kokko, 2010, for an analysis of parent-offspring conflict). It is less well  
278 appreciated that the mother must also invest in the dispersal ability of its offspring (e.g. Wheelwright  
279 & Logan, 2004). Such an investment will necessarily come at a cost, i.e it will trade off with fertility  
280 or survival. It has been shown in other contexts that trade-offs may shape the evolution of dispersal  
281 considerably (e.g. Roff, 1994; Burton *et al.*, 2010; Travis *et al.*, 2010; Fronhofer *et al.*, 2011; Travis  
282 *et al.*, 2012). We here demonstrate for sessile organisms that trading fecundity for an increased survival  
283 of dispersing offspring, i.e. maternal investment, characteristically influences the form of the dispersal  
284 kernel. Particularly for high dispersal costs bimodal kernels emerge and, at the same time, the kernels  
285 become heavily fat-tailed. In contrast to previous studies that already demonstrate the evolution of  
286 bimodal distance pdfs (Starrfelt & Kokko, 2010) our model demonstrates the evolution of bimodality in  
287 both density and distance pdfs. These results prove to be robust against variation in all tested model  
288 parameters (figures 4 and supporting information). They even hold if the offspring were to pay a part of  
289 dispersal costs themselves (supporting information S3).

290 By relaxing the somewhat arbitrary assumption of a world with discrete habitat patches and modelling

291 inter-individual competition explicitly at the individual level in continuous space through a competition  
292 kernel, our results represent an important step towards a better understanding of dispersal in sessile  
293 organisms such as plants. Our results from scenarios in which offspring pay distance-dependent dispersal  
294 costs (figure 2 A, B) are in good accordance with findings from Rousset & Gandon (2002). Yet, they  
295 show some distinct differences as our model assumes distance-dependent competition (competition ker-  
296 nels), maternal control of dispersal and overlapping generations. Due to decreasing kin competition and  
297 increasing (saturating) dispersal costs Rousset & Gandon (2002) also predict unimodal dispersal kernels  
298 in two-dimensional landscapes. By explicitly introducing competition for space we can show that the  
299 width of the competition kernel ( $\sigma$ ) will determine the location of the kernel's peak. Depending on their  
300 specific shape competition kernels may even increase tail weight since competitive interactions are not  
301 limited to the size of an arbitrarily defined grid-cell. Generally, our kernels are slightly more fat-tailed as  
302 we assume maternal control of dispersal (Starrfelt & Kokko, 2010) in comparison to Rousset & Gandon  
303 (2002). Finally, when offspring pay dispersal costs our model predicts that all offspring will disperse (fig-  
304 ure 2 A, B; the first distance class has a zero value) because the competition kernel drives all seeds away  
305 from the maternal individual. This will not necessarily hold for grid based models, especially if one grid  
306 cell may contain more than one individual. Rousset & Gandon (2002) for example, do predict a certain  
307 amount of non-dispersers. This effect is especially strong, as the modelled organisms are assumed to be  
308 annual in contrast to our model. For the same reasons Starrfelt & Kokko (2010) do not find unimodal  
309 kernels.

310 In scenarios with maternal investment bimodality of the dispersal kernel emerges mainly because of  
311 two mechanisms: (i) as the mother pays dispersal costs defined by the dispersal kernel (equation 2)  
312 increasing the variance of the kernel through a bimodal distribution with a peak at zero (or at very small  
313 distances) allows the mother to decrease the costs while keeping the mean dispersal distance constant  
314 or even increasing it through a heavily fat tail. Thus, by reducing the dispersal distances of some  
315 offspring the mother may achieve LDD for other propagules. Higher dispersal distances are evolutionarily  
316 advantageous because they minimize kin competition (Hamilton & May, 1977; Rousset & Gandon, 2002)  
317 an effect known to be especially pronounced for maternal control of dispersal (Hamilton & May, 1977;  
318 Starrfelt & Kokko, 2010) . (ii) Furthermore, the maternal location has an interesting attribute that  
319 makes it attractive for seed deposition. In case of the mother's death it characteristically implies a  
320 minimal influence of the nearest neighbours' competition kernels (see figure 1, thin black line). Locally it  
321 maximizes an individual's survival and non-dispersers will be able to inherit this locally optimal location  
322 ('territorial inheritance') after the mother's death.

323 It is immediately clear that the latter mechanism will be critically dependent on the assumed width  
324 of the first distance class. We therefore tested the impact of increasing the extent of this first class. Our

325 tests show that the bimodality reported here does indeed vanish for coarse grids but is stable for a width  
326 of the first distance class ( $d_1$ ) of up to  $0 \leq d \leq 0.2$  (see also figure 1). This results underlines the possible  
327 artifacts resulting from grid-based models in general.

328 The two mechanisms discussed above also explain the influence of the age-specific component of  
329 the competition kernel (figure 4) and of fecundity (see supporting information S1). Increased local  
330 competition through fast growth leads to a reduction of kernel bimodality in scenarios with maternal  
331 investment. Although there is an advantage for mothers keeping a fraction of offspring close by for  
332 territorial inheritance fast growth leads to an important increase in local competition between the mother  
333 and her non-dispersing offspring and between these. This leads to a reduction to the peak at distance  
334 zero, i.e. the number of non-dispersers. The same effect will emerge from increased numbers of offspring.  
335 As the kernel costs resulting from the formation of a fat-tail are offset by the production of ‘cheaper’  
336 non-dispersers, reducing the latter will lead to a reduction of tail weight.

337 Due to asymmetric competition between the mother and the offspring a majority of non-dispersers  
338 may actually die. This of course begs the question why mothers produce these offspring in the first place.  
339 If this was just a strategy to spare resources for the production of more expensive long-distance dispersers  
340 and these ‘cheap’ propagules were thus only produced to reduce the costs of offspring production, mothers  
341 could as well simply reduce the number of offspring produced and put all resources into long-distance  
342 dispersers. In order to explore this question we ran additional numerical analyses including evolvable  
343 fecundities and a trade-off between fecundity and baseline mortality (supporting information S5 and  
344 S6). Individuals reducing their fecundity could thus increase their survival. In all these model runs, the  
345 bimodality was evolutionarily stable (supporting information S5). Regardless of the form of the assumed  
346 trade-off function (concave, linear, convex) we observed evolution towards short lived, sometimes annual,  
347 but very fecund individuals showing an increasingly bimodal kernel (supporting information S6). Dytham  
348 & Travis (2006) analyse the concurrent evolution of longevity and dispersal distance. Their results show  
349 that shorter life spans lead to shorter dispersal distances. Although our model is significantly different,  
350 the increasing bimodality, i.e. the higher frequency of non-dispersers we find is a similar phenomenon. It  
351 results from reduced kin competition and the possibility of territorial inheritance. Yet, as the form of our  
352 kernel may evolve freely, a reduced life span does not lead to smaller dispersal distances in general. On  
353 the contrary, as noted above, in scenarios with maternal investment the kernels are bimodal and heavily  
354 fat-tailed with an important fraction of long-distance dispersers.

355 Interestingly the occurrence of a bimodal kernel that generates non-dispersers and long-distance dis-  
356 persers parallels the co-occurrence of philopatrics and dispersers found in models of actively moving  
357 organisms that include a trade-off between fertility and dispersal ability (e.g. Roff, 1994; Fronhofer *et al.*,  
358 2011). Yet, as these models assume offspring control of dispersal and consider emigration rates only, the

359 underlying mechanisms are different (see also below). In recent work that incorporates such a trade-off  
360 into an explicit movement model Travis *et al.* (2012) show that emigration rates increase for high levels  
361 of investment. Although we also find more LDD in our model emigration rates actually decrease which  
362 is due to the kernel’s bimodality.

363 In general, maternal investment, i.e. trading fecundity for an increased survival of dispersing offspring,  
364 is highly advantageous. It allows the persistence of stable populations despite low fecundities, high  
365 mortalities and high competition, conditions that otherwise lead to global extinctions. This can be seen,  
366 e.g., in the supporting information figure S1 A–D: for low fecundities and if the offspring pay distance  
367 dependent dispersal costs populations are not viable for dispersal costs  $\mu_d^0 > 0.3$ . This is not the case  
368 in scenarios with maternal investment. Additional numerical analyses show that maternal investment  
369 allows populations to survive dispersal costs over 0.8 (not shown). Simulation experiments also show that  
370 the ‘mother pays’ strategy is evolutionarily stable (supporting information S4).

371 To summarize so far and put our results in a broader context, if the offspring control dispersal the  
372 evolutionarily stable kernel must guarantee equal fitness expectations for all offspring (see Rousset &  
373 Gandon, 2002). This logic does not apply if dispersal is controlled maternally as we assume in this  
374 study: the parent-offspring conflict (discussed in the context of dispersal distances in Starrfelt & Kokko,  
375 2010) leads to larger dispersal distances, as the maternal individual maximizes its own inclusive fitness  
376 expectations by reducing kin competition. If the offspring pay dispersal costs, these costs are the only  
377 mechanism that restrain dispersal distance and counteract the effect of (kin) competition which drives  
378 seeds away from the maternal individual. This cost-benefit calculation is fundamentally changed if the  
379 mother also pays dispersal costs. Increasing dispersal costs lead to selection for non-dispersers in spite  
380 of strong competition with the maternal individual, as this allows the mother to reduce its investment in  
381 propagule dispersal ability, which in turn allows for more LDD. Simultaneously, selection seems to favour  
382 a reduction in longevity for an increase in fecundity. Ultimately, this may lead to highly fertile annual  
383 organisms with strongly bimodal dispersal kernels (see supporting information S5 and S6).

## 384 **Examples**

385 Our model is applicable to sessile organisms such as plants. Most plants will show maternal investment,  
386 at least to some degree, since fruit and seed production is obviously maternally regulated. The bimodal  
387 dispersal kernel which we predict can be realized for example by seed polymorphisms, a phenomenon  
388 that has been frequently observed (for a review, see Imbert, 2002). The Asteraceae *Heterotheca latifolia*  
389 for example shows a dimorphism in achene structure: while disc achenes, which have a pappus, are wind  
390 dispersed and responsible for LDD ray achenes are not (Venable & Levin, 1985). This polymorphic seed  
391 structure will lead to bimodality in the dispersal kernel and increased tail weight (see also van Mølken

392 *et al.*, 2005; Brändel, 2007). The same effect can be achieved by polychory, i.e. the use of more than  
393 one seed dispersal agent (e.g., Berg, 1966; Jordano *et al.*, 2007; Russo *et al.*, 2006). For example in  
394 *Prunus mahaleb* small birds are responsible for short distance dispersal while fruits eaten by mammals  
395 and larger birds are dispersed over long distances (Jordano *et al.*, 2007). In addition our results are  
396 in good accordance with the increasing evidence that multiple seed size strategies, directly leading to  
397 different dispersal distances, may generally be due to life-history trade-offs (competition-colonization or  
398 stress tolerance-fecundity trade-offs, see e.g. Jakobsson & Eriksson, 2003; Lönnberg & Eriksson, 2013).  
399 Of course, in purely wind-dispersed plants with monomorphic seeds such as e.g. modelled by Travis  
400 *et al.* (2010) trade-offs may also occur e.g. between plant height which influences dispersal distance and  
401 fertility. Such trade-offs may then lead to the evolution of different plant heights depending e.g. on  
402 habitat availability or local extinctions.

403 In a very broad sense our results may be of significance for territorial animals, although the model  
404 has not been designed for actively moving animals. Of course, in this case competition will be more  
405 prone to act on fertility than on mortality, but the resulting patterns may be similar. A dimorphism can  
406 often be observed between non-dispersers that wait, eventually help their parents, and bet on territorial  
407 inheritance and dispersers that try to colonize new, eventually empty territories (e.g. Kokko & Ekman,  
408 2002).

## 409 **Simplifications**

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

421 Evidently, dispersal could also occur through time (dormancy). Trade-offs and correlations between  
422 dormancy, longevity and spatial dispersal have been analysed theoretically and empirically (e.g. Rees,  
423 1993). These additional complexities are far beyond the scope of this article and will not be discussed in  
424 detail here. Note that dormancy as a bet-hedging strategy is especially relevant in variable environments

425 (for a review see e.g. Childs *et al.*, 2010) that are not in the focus of this study.

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

## 441 **Conclusions**

442 Although the concept of a dispersal kernel is not new only little work has been done on the evolution of  
443 the shape of dispersal kernels. In contrast to previous work (Hovestadt *et al.*, 2001; Rousset & Gandon,  
444 2002; Starrfelt & Kokko, 2010) we have concentrated on two important aspects that have received little  
445 attention in this context up to now: (i) the effects of individual competition kernels in continuous space  
446 and (ii) maternal investment. We predict the emergence of heavily fat-tailed and bimodal dispersal  
447 kernels for sessile organism with overlapping generations.

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## 575 Table and figure captions

### 576 Table 1:

577 Important model parameters, their meaning and tested values.

578

### 579 Figure 1:

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

590

### 591 Figure 2:

592 Maternal investment and the evolution of dispersal kernels. All four panels show evolutionarily stable  
593 dispersal kernels (distance pdfs). The upper row (A, B) depicts the influence of dispersal costs without  
594 maternal investment, i.e. when offspring pay distance-dependent dispersal costs according to equation 1.  
595 The competition kernel (equation 4) leads to unimodal and fat-tailed distributions (A). Increasing disper-  
596 sal costs lead to narrower and more peaked kernels (B). The lower row (C, D) shows kernels for scenarios  
597 with maternal investment, i.e. the mother pays kernel-dependent dispersal costs (equation 2) and reduces  
598 her fecundity in order to maximize offspring survival during dispersal (equation 3). Maternal investment  
599 leads to heavily fat-tailed kernels and to bimodality at high dispersal costs (D). The inset in panel D  
600 shows the same numerical analysis for an increased resolution of the dispersal kernel (distance class extent  
601 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  $\mu_d^0 = 0.1$

602 (left panels; A, C) or  $\mu_d^0 = 0.4$  (right panels; B, D).

603

604 **Figure 3:**

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

614

615 **Figure 4:**

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

## Tables and Figures

Table 1

<b>parameter</b>	<b>values</b>	<b>meaning</b>
$\lambda_0$	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)

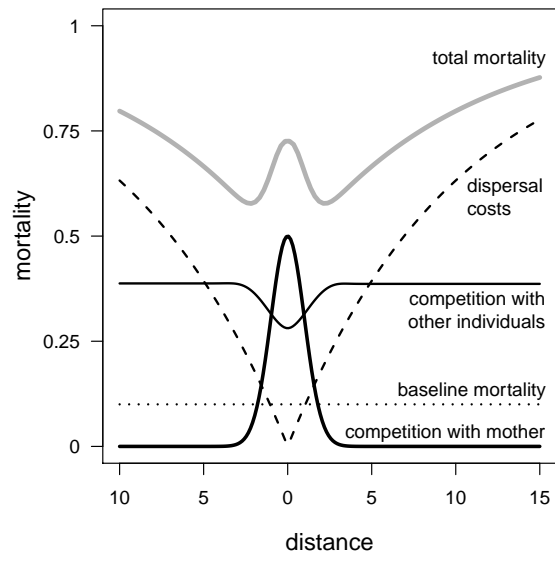


Figure 1



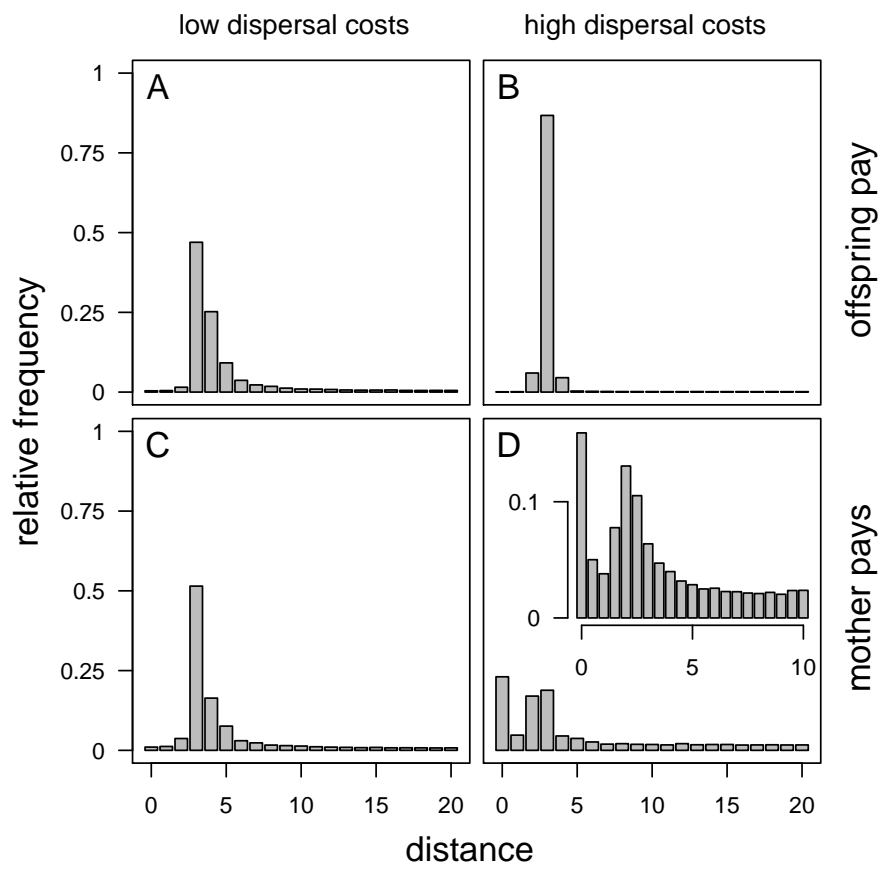


Figure 2

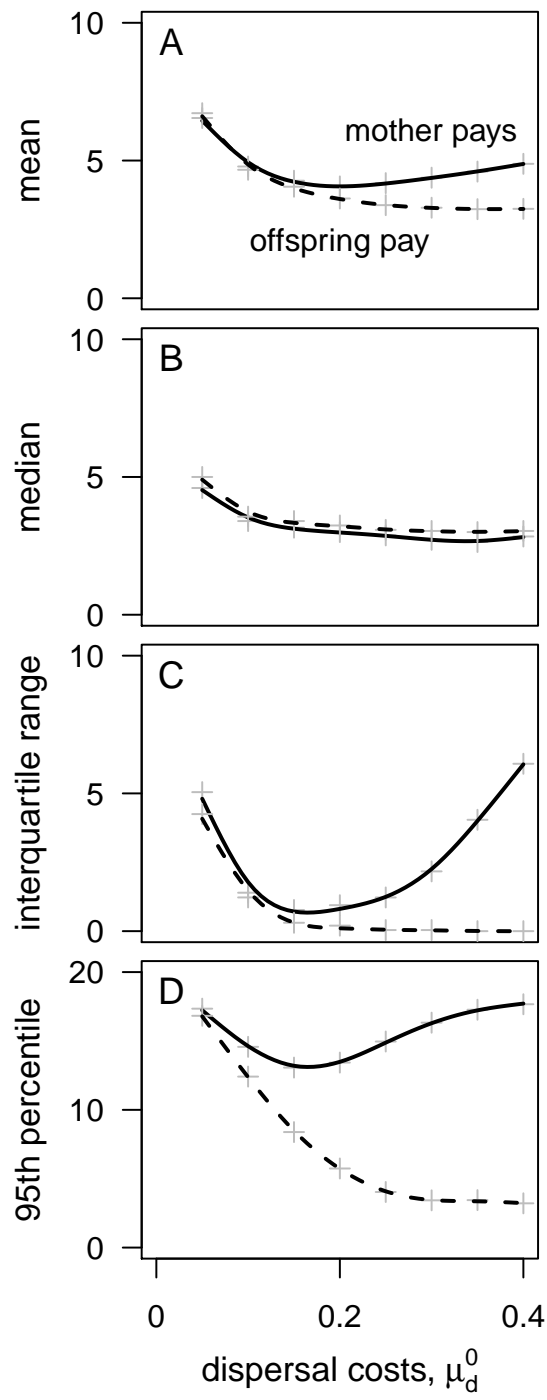


Figure 3

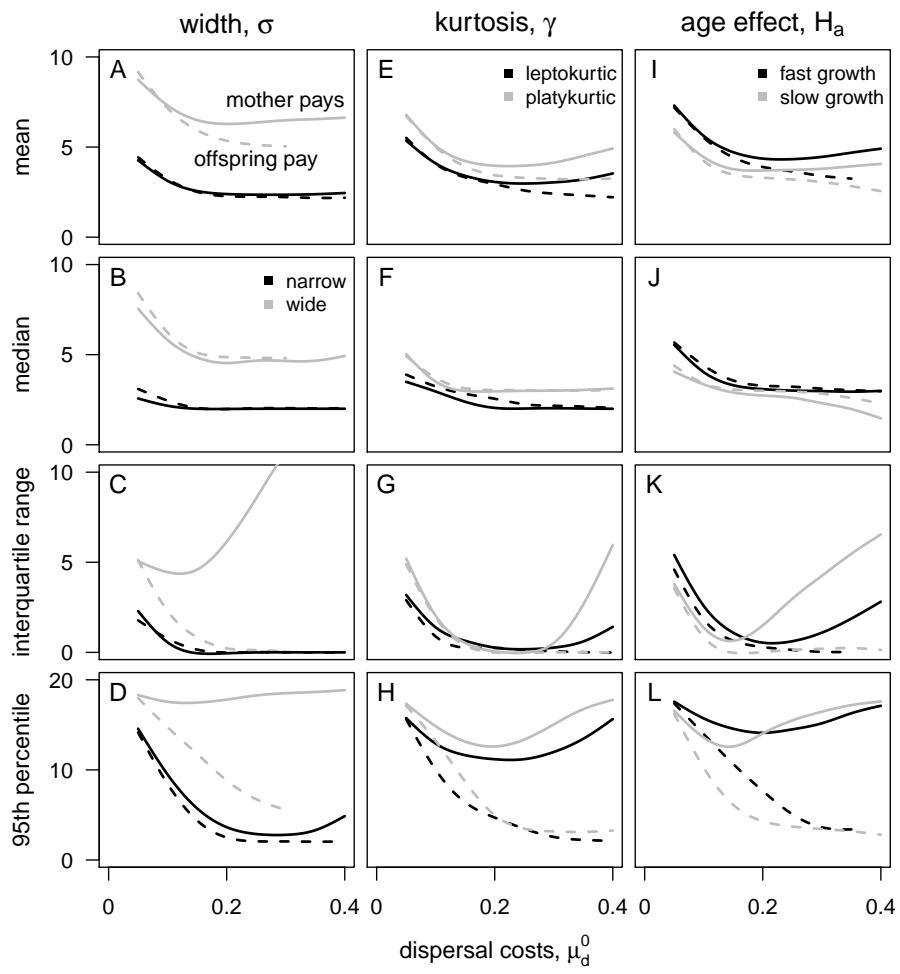


Figure 4

# 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

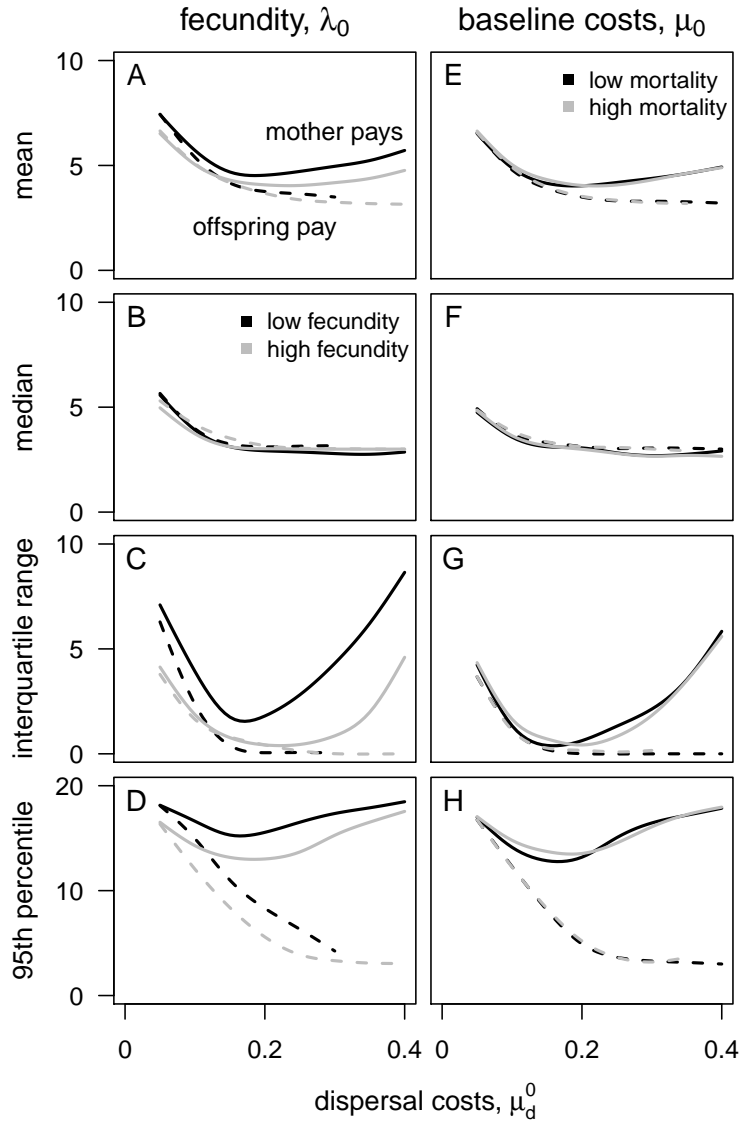


Figure S1: Influence of fecundity and mortality. Solid lines show results for scenarios with maternal investment (‘mother pays’) and dashed lines without (‘offspring pay’). Black curves always indicate scenarios in which the focal parameter value was halved and grey curves scenarios in which the value was doubled. Low fecundities ( $\lambda_0$ ) underline the effects described above (A–D), but higher fecundities do not destroy the patterns, i.e., 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:  $\lambda = 0.3$ ).

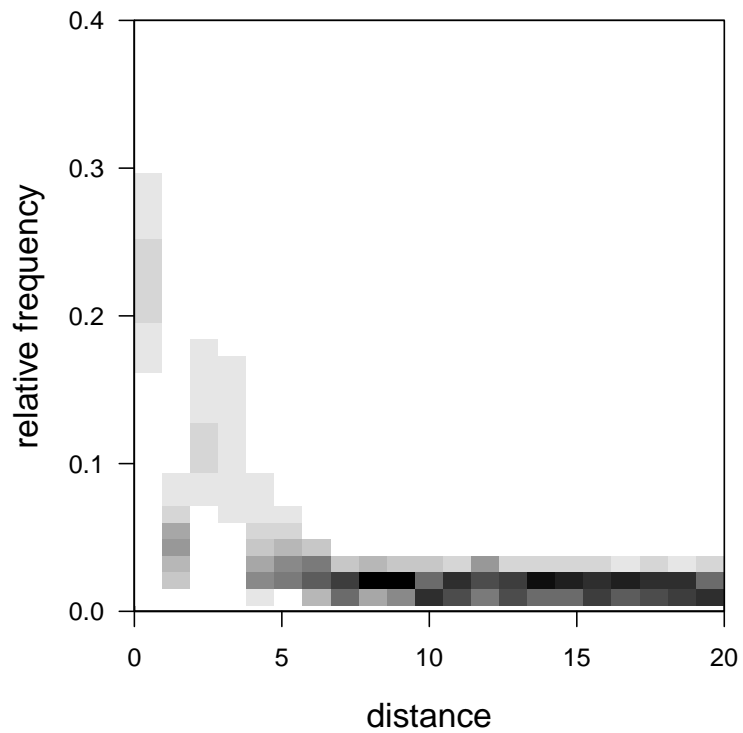


Figure S2: Evolutionarily stable dispersal kernel as a 2D histogram. This figure corresponds to figure 2 D and shows the strategies of all individuals across all 25 replicate simulation runs. Clearly, the bimodality occurs at the individual kernel level and is not a result of a mixed strategy at population level. Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.4$ .

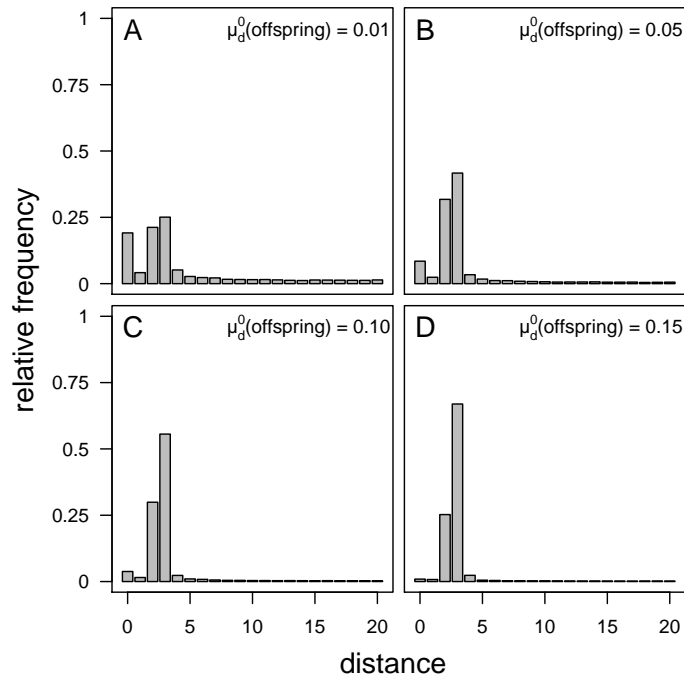


Figure S3: Maternal investment and the evolution of dispersal kernels. All four panels show evolutionarily stable dispersal kernels (distance pdfs) for scenarios with maternal investment, i.e. the mother pays kernel-dependent dispersal costs. Additionally, different level of direct dispersal costs paid by the offspring are included. These results show that if both, mother and offspring, have to pay dispersal costs our results hold up to a considerable amount of costs paid by both. Parameters:  $\lambda_0 = 4$ ,  $\mu_0 = 0.1$ ,  $\gamma = 2$ ,  $\sigma = 1$ ,  $H_a = 3$ , and  $\mu_d^0 = 0.4$  for the mother.

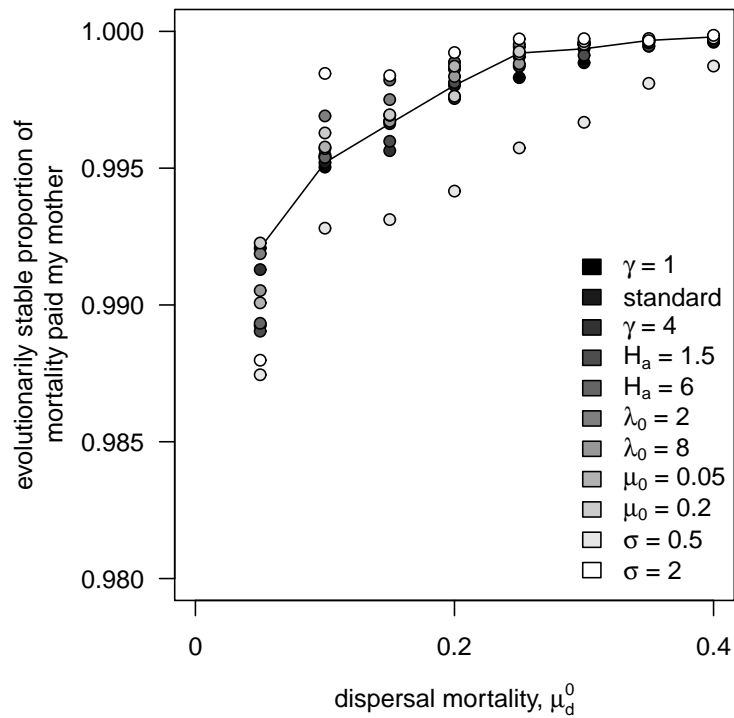


Figure S4: Evolutionarily stable allocation of dispersal costs to mother vs. offspring. We here allowed the allocation of costs to be itself an evolvable trait: depending on this trait a proportion of the distance dependent dispersal costs ( $\mu_d^0$ ) is paid by the mother and the remaining costs are 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.

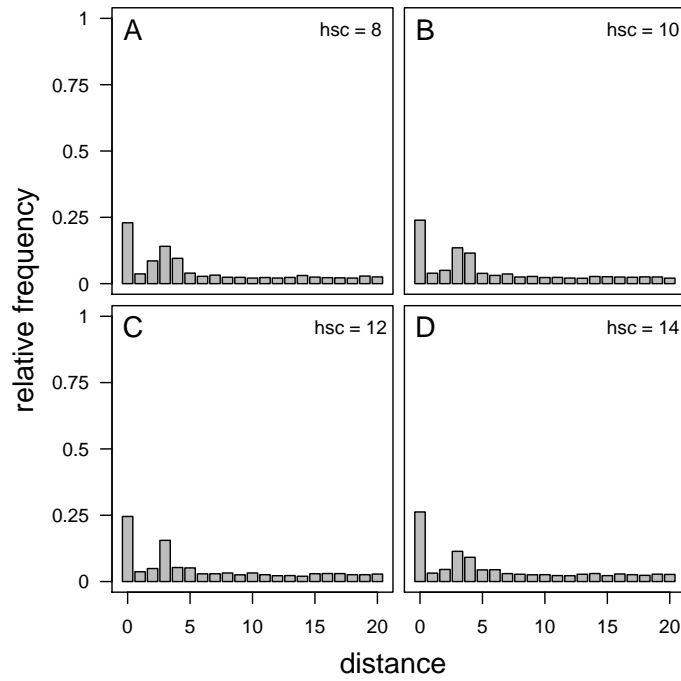


Figure S5: Maternal investment, baseline mortality - fertility trade-off, and the evolution of dispersal kernels. All four panels show evolutionarily stable dispersal kernels (distance pdfs) for scenarios with maternal investment, a trade-off between baseline mortality and fecundity and evolving fecundities. 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  $\mu_d^0 = 0.4$ .



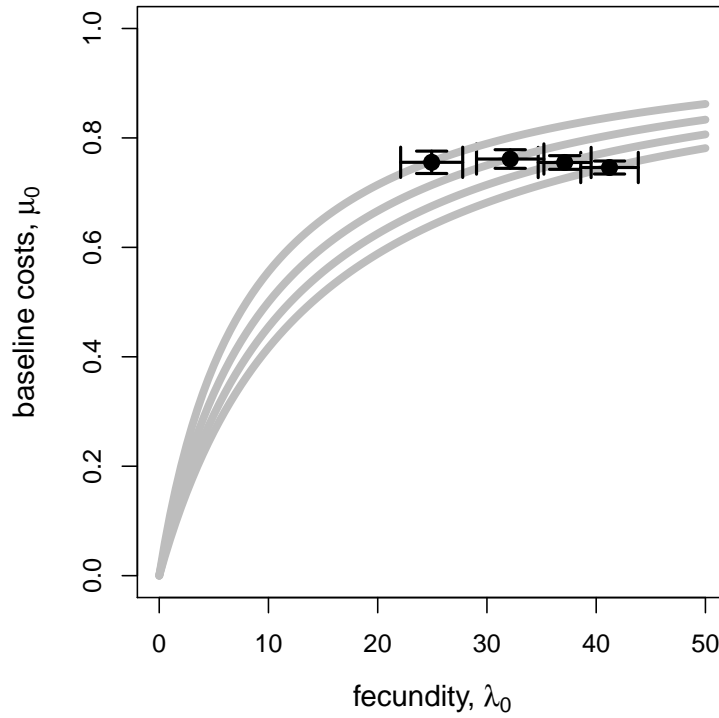


Figure S6: Maternal investment, baseline mortality - fertility trade-off, and the evolution of dispersal kernels. The figure shows the evolutionarily stable fertility (mean and standard deviation) and the corresponding baseline mortality for scenarios with maternal investment and a trade-off between 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  $\mu_d^0 = 0.4$ .