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**BONTE, D.**, HOVESTADT, T. & POETHKE, H.-J. (2010).

Oikos 119: 560-566

**To refer to or to cite this work, please use the citation to the published version:**

**BONTE, D.**, HOVESTADT, T. & POETHKE, H.-J. (2010). Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. Oikos 119: 560-566.

**Doi:** 10.1111/j.1600-0706.2009.17943.x

1 **Evolution of dispersal polymorphism and local adaptation of dispersal distance in**  
2 **spatially structured landscapes**

3

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## 1 **Abstract**

2 Many organisms show polymorphism in dispersal distance strategies. This variation is particularly  
3 ecological relevant if it encompasses a functional separation of short- (SDD) and long-distance  
4 dispersal (LDD). It remains, however, an open question whether both parts of the dispersal kernel are  
5 similarly affected by landscape related selection pressures.

6

7 We implemented an individual-based model to analyze the evolution of dispersal traits in fractal  
8 landscapes that vary in the proportion of habitat and its spatial contagion. Individuals are  
9 parthenogenetic with dispersal distance determined by two alleles on each individual's genome: one  
10 allele coding for the probability of global dispersal and one allele coding for the variance  $\sigma$  of  
11 Gaussian local dispersal with mean value zero.

12

13 Simulations show that mean distances of local dispersal and the probability of global dispersal,  
14 increase with increasing habitat availability, but that changes in the habitat's spatial autocorrelation  
15 impose opposing selective pressure: local dispersal distances decrease and global dispersal  
16 probabilities increase with decreasing spatial autocorrelation of the available habitat. Local  
17 adaptation of local dispersal distance emerges in landscapes with less than 70% of clumped habitat.

18

19 These results demonstrate that long and short distance dispersal evolve separately according to  
20 different properties of the landscape. The landscape structure may consequently largely affect the  
21 evolution of dispersal distance strategies and the level of dispersal polymorphism.

22

## 1 **Introduction**

2 Dispersal has important ecological and evolutionary consequences for organisms living in spatially  
3 structured populations (Kokko & López-Sepulcre 2006). It plays therefore a crucial role in the context  
4 of habitat fragmentation. Dispersal has repeatedly been shown to be a plastic process conditional on  
5 the individual's social and ecological environment (Clobert et al. 2009). Further, the presence of  
6 heritable variation and strong selection pressures related to e.g. landscape composition may induce  
7 fast evolution in dispersal traits (for reviews see Bowler & Benton 2005, Kokko & López-Sepulcre  
8 2006, Ronce 2007). The dispersal strategy should be considered as an integrated process,  
9 encompassing dispersal propensity as well as transfer and settlement, the latter two being reflected  
10 in an individual's effective displacement distance.

11  
12 Three kinds of mechanisms have been shown to favor the evolution of increased dispersal rates: kin  
13 competition (e.g., Hamilton & May 1977, Frank 1986, Taylor 1998, Ronce et al. 2000, Poethke et al.  
14 2007), inbreeding avoidance (e.g., Waser et al. 1986, Gandon 1999) and environmental stochasticity  
15 in space and time (e.g. Van Valen 1971, Olivieri et al. 1995, FriedenberG 2003, Poethke et al. 2003).  
16 Evidently, these benefits are balanced by intrinsic or landscape-related dispersal costs (e.g., McPeck &  
17 Holt 1992, Travis & Dytham 1999, Heino & Hanski 2001, Poethke & Hovestadt 2002, Poethke et al.  
18 2003). Although the evolution of dispersal distance has received far less attention, the available  
19 studies (Rousset & Gandon 2002 for kin competition, Hovestadt et al. 2001 for relationship with  
20 dispersal mortality, Murell et al. 2002 for correlations with subpopulation dynamics), point out that  
21 mechanisms that act on the evolution of emigration rates may equally affect the evolution of  
22 dispersal distance. It is therefore reasonable to assume that the spatial extent of these selective  
23 forces will affect the evolution of increased dispersal distances as well. Because dispersal propensity  
24 and dispersal distance determine gene-flow, they may strongly interfere with, and often constrain,  
25 processes of local adaptation and trait polymorphism in natural landscapes (Lenormand 2002, Billiard  
26 & Lenormand 2005, Garant et al. 2007). Thus, dispersal may be subject to local adaptation (Hovestadt  
27 et al. 2001, Gros et al. 2006) and may, at the same time, influence spatial patterns in local adaptation  
28 and its evolution.

1

2 Many organisms show polymorphism in dispersal distance strategies. Animals may disperse by  
3 different mechanisms in the larval life phase compared to the adult stage (Ghent 1999, Bonte et al.  
4 2007). Many anemochorous (i.e., wind dispersed) plants show distinct seed dimorphism with heavy  
5 short-distance dispersing seeds and light seeds with pappus-structures for long-distance aerial  
6 dispersal (Imbert 2001, Cheptou et al. 2008), may ‘exploit’ different dispersal vectors like birds with  
7 small and large home-ranges, or plants may either distribute clonally by stolones or by seeds (e.g.,  
8 Gardner & Mangel 1999).

9

10 The dispersal polymorphism is of particular ecological relevance if it encompasses a functional  
11 separation of short- and long-distance dispersal (further on abbreviated as respectively SDD and LDD).  
12 Presumably, such different dispersal modes are characterised by different cost-benefit ratios due to  
13 evolutionary and environmental constraints (Bonte et al. 2006). Therefore different parts of the  
14 dispersal kernel may evolve independently (Ronce 2007, Bonte et al. 2008). For instance, long  
15 distance dispersal (i.e., dispersal beyond the bounds of the local habitat cluster) can be considered to  
16 be most advantageous in landscapes with high habitat availability or under conditions with strong  
17 enemy interactions (Hovestadt et al. 2001, Muller-Landau et al. 2003).

18

19 At large spatial scales, we can expect that polymorphisms in dispersal strategies are maintained by  
20 among-landscape variation in environmental stochasticity, habitat quality and dispersal mortality.  
21 Even at smaller spatial scales, i.e. within metapopulations, polymorphism in dispersal may evolve as a  
22 consequence of local adaptation towards local habitat configuration. This was empirically  
23 demonstrated by Hanski et al. (2004) and Bonte et al. (2006). These fast evolutionary responses  
24 towards local landscape structure are important for species conservation because they may either  
25 rescue or hasten species extinction through genetic and demographic feedbacks. This has for instance  
26 been shown by Colas et al. (1997) for an extremely rare, endemic cliff-dwelling plant species. Within  
27 single patches of habitat, recent modelling work (Gros et al. 2006) suggests that local adaptation in  
28 dispersal strategies may only evolve beyond a minimum patch size at the edges of patches.

29

1 While insights into dispersal evolution are predominantly delivered by modeling and microcosm  
2 experiments in simple landscapes, field studies highlight the importance of landscape structure for  
3 dispersal evolution (e.g., Hill et al. 1999, Hanski et al. 2004, Bonte et al. 2006, Merckx & Van Dyck  
4 2006, Schtickzelle et al. 2006, Bonte et al. 2007, Cheptou et al. 2008). According to this empirical  
5 work, low dispersal distances in habitat embedded in hostile matrix (isolated habitat, edges) and high  
6 dispersal distances in continuous habitat are hypothesised to be an adaptation to the local landscape  
7 structure. Our understanding of dispersal evolution and the environmental conditions for local  
8 dispersal adaptation within realistic landscapes needs consequently to be bridged by theoretical  
9 studies. Therefore, we developed a spatially explicit, individual based model for dispersal in fractal  
10 landscapes differing in their degree of habitat availability and habitat clumping (With & King 1997).  
11 These are useful to assess the evolution of dispersal distance in a conceptual, though realistic way  
12 (With 1997). We explicitly address the question how changes of both, habitat availability and its  
13 spatial autocorrelation or contagion affect the evolution of dispersal distance polymorphism, by  
14 inferring dispersal kernels that are a function of two different dispersal functions. In contrast to  
15 earlier theoretical work (Hovestadt et al. 2001, Murell et al. 2002, Rousset & Gandon 2002), we here  
16 explored under which landscape configurations adaptive polymorphisms in dispersal distance strategy  
17 emerge.

18

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## 1 **Material and Methods**

### 2 **Neutral landscapes**

3 We used the program QRULE (Gardner 1999, Gardner & Urban 2007) to generate spatially structured  
4 landscapes. The generated landscape models are binary (i.e., only with a binary distinction between  
5 suitable habitat and unsuitable matrix) and measure 256 x 256 grid cells. For details on the landscape  
6 generator algorithm we refer to Gardner (1999). In short, we used fractal landscapes that are  
7 generated using the mid-point displacement algorithm in which both the fraction ( $P$ ) and the degree  
8 of spatial autocorrelation ( $H$ ) can be controlled.  $H$  represents the spatial autocorrelation or clumping  
9 of habitat, with low values indicating dispersed distribution of habitat cells; high values represent a  
10 strongly aggregated habitat distribution (With 1997). It should be noted that such fractal landscapes  
11 are always clumped and never overdispersed as compared to a pure Poisson process. Nevertheless  
12 we will use the term "clumped" for highly autocorrelated (large values of  $H$ ) and "dispersed" for less  
13 autocorrelated (low  $H$ ) landscapes. Fig. 1 provides examples of four landscapes differing clumping ( $H$ )  
14 and fraction of suitable habitat ( $P$ ). Fractal landscapes provide a tool to tease apart the effects of  
15 habitat fragmentation (with high values of  $H$  indicating strong connectivity) from habitat loss (with  
16 high values of  $P$  indicating high amounts of preserved habitat). To avoid edge effects in the  
17 simulations, landscapes were wrapped at the edges into a torus so that edges matched, and can  
18 consequently be considered as being infinite but periodic landscapes.

19  
20 We investigated the evolution of dispersal distance in fractal landscapes that systematically varied in  
21  $P$  between 0.1 and 0.9 and  $H$  between 0 and 1 (Table 1). Intervals were 0.1 in both cases,  
22 subsequently resulting in 99 landscapes with different combinations of  $H$  and  $P$ . We chose to generate  
23 5 replicates of 99 interdependent landscape (the landscapes are generated from the same baseline  
24 fractal landscape; Gardner 1999). Consequently, a total of 495 simulations (described hereunder)  
25 were run.

26

### 27 **The model**

28 **Individuals** - We modelled the evolution of dispersal distance in parthenogenetic organisms with  
29 discrete generations. Individuals either disperse globally with a certain probability (i.e., the individual

1 is displaced toward a random cell in the landscape), or they draw a distance from a Gaussian  
 2 probability distribution (see below). We chose to implement this dispersal function because (i) it  
 3 allows the generation of fat-tailed dispersal kernels by increased global dispersal and (ii) because of  
 4 its realism in many terrestrial arthropods with polymorphic dispersal strategies (Zera & Denno 1997).  
 5 Dispersal costs emerge in first instance due to arrival in unsuitable matrix cells, but we alternatively  
 6 tested a scenario with additional distance dependent dispersal mortality  $\mu_{disp}$ . The latter is positively  
 7 linearly correlated with dispersal distance according to the rule  $\mu_{disp} = \text{dist}/\text{dist}_{\max}$ . In our landscape of  
 8 256 x 256 grids,  $\text{dist}_{\max}$  equals 362.

9

10 **Local population dynamics** – Each habitat grid cell was characterised by a carrying capacity  $K$  beyond  
 11 which reproduction failed (table 1). Reproduction takes place after dispersal, i.e. after the building-up  
 12 of local densities ( $\delta$ ). The realised number of offspring  $\lambda$  was determined as a linear function of the  
 13 local density  $\lambda = K/\delta$ , with complete loss of individuals through failed reproduction when  $\delta \geq K$  in  
 14 local grid cells, but with the possibility for recolonization from reproducing individual in the  
 15 landscape. Individuals die immediately when they disperse into the hostile matrix. These local  
 16 population dynamics resemble typical arthropod herbivores with distinct genetically determined  
 17 dispersal polymorphism and scramble competition (Zera & Denno 1997).

18

19 Alternatively, we tested the model for logistic growth population dynamics (i.e. contest  
 20 competition), hypothesised to plant systems. Therefore, we modified local population dynamics  
 21 according to Hassell & Comins (1976). Local population dynamics are governed by density-dependent  
 22 reproduction of individuals. Each generation, a female gives birth to  $\lambda$  offspring, where  
 23  $\lambda \sim \text{Pois}(\lambda)$ . In our simulations,  $\lambda$  was set to 2, typical for arthropod demography (Bellows 1981).  
 24 Offspring develop into mature individuals with a density-dependent survival probability  $s$  due to  
 25 contest competition:

$$26 \quad s = \frac{1}{(1 + a\delta)} \quad (1) \quad \text{with } a = \frac{\lambda - 1}{K}$$

27 Here  $\delta$  represents the local population density and  $K$  carrying capacity.

28



1 **Evolution of dispersal** – Dispersal distance is determined by two alleles on each individual’s genome:  
 2 one allele (allele  $G_p$ ) coding for the probability of global dispersal  $p_{\text{global}}$ . Alternatively, that is with  
 3 probability  $1 - p_{\text{global}}$  individuals will disperse locally according to a Gaussian dispersal kernel (mean  
 4 value of 0) with the genetically determined variance ( $\sigma$ ). The Gaussian kernel is two-dimensional with  
 5 randomly selected directionality. Thus the second allele ( $G_g$ ) codes for the variance ( $\sigma$ ) of the  
 6 Gaussian distribution.  $G_p$  Individual allele frequencies were initialised from a uniform distribution  
 7 [0..1], and for  $G_g$  from a uniform distribution [1..128]. Offspring inherit both alleles from their parent,  
 8 but alleles may mutate with a probability of 0.001. Mutations are uniformly sampled within the  
 9 interval  $0.9 \cdot x$  to  $1.1 \cdot x$ . As a consequence, all individuals are theoretically dispersing, but philopatry  
 10 (dispersal with distance zero) occurs when both  $G_p$  and  $G_g$  approach zero.

11

## 12 **Data analysis**

13 Stable distributions of trait values were reached within 1000 time-steps in all scenarios. Mean trait  
 14 values were calculated for all surviving individuals in one landscape. Beyond the global evolutionary  
 15 results we were also interested to investigate under which conditions local adaptation of dispersal  
 16 traits can occur. To characterize local conditions, we estimated the proportion habitat cells ( $p'$ ) in the  
 17 vicinity of 1000 randomly selected habitat cells in a similar way as the developed univariate O-ring  
 18 statistics by Wiegand et al. (1999). The number of suitable habitat cells in 100 increasing radii of 1 grid  
 19 cell was counted for each of these randomly selected cells. In a fractal landscape the availability of  
 20 habitat is expected to more or less gradually decline with distance for any cell of suitable habitat,  
 21 ultimately equilibrating at the proportion of available habitat in the entire landscape ( $P$ ). We use the  
 22 slope  $\alpha$  of the fitted negative exponential function  $p' = e^{-(\alpha \cdot \text{radius})}$  to describe the change in habitat  
 23 availability with distance for the individual cells, with high values representing steeply declining  
 24 availability (as would be the case for isolated patches in the landscape, or patches at edges of  
 25 clumped habitat cells). Intermediate values of  $\alpha$  indicate gradually declining habitat availability, while  
 26 values of  $\alpha$  close to 0 would indicate a homogeneous habitat distribution within the landscape sector  
 27 analyzed. In a region with rapidly declining habitat availability (large  $\alpha$ ) it should be beneficial to limit  
 28 local dispersal to the near vicinity, i.e. selection should favour low levels of the allele  $G_g$ . We thus use

1 the strength of the Spearman rank correlation ( $R_s$ ) between the cell's value for  $\alpha$  (a habitat attribute)  
2 and the values of the two dispersal alleles ( $G_p$  respectively  $G_g$ ) of the individual residing in this cell to  
3 estimate the degree of local adaptation (or selection driven polymorphism). We assume the presence  
4 of local adaptation only when  $R_s^2 > 10\%$ .

5

6 Mean individual trait values and Spearman correlations between local trait values and local landscape  
7 structure were subsequently averaged over the five independent replicas for each landscape type  
8 (i.e., each landscape determined by one of the 99  $H,p$ -values). These averaged trait values are  
9 presented in this contribution.

10

11

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13

14

## 1 **Results**

2 Evolutionary stable Gaussian dispersal distances (Fig 2 A,C,E) evolve towards higher values with an  
3 increase in the proportion of available habitat ( $P$ ) as well as with an increase in spatial autocorrelation  
4 ( $H$ ). The proportion of individuals performing global dispersal also increases with increasing  $P$  but  
5 declines with increasing  $H$  (Fig. 2B,D,F), i.e. selection favours the investment into local dispersal as  
6 autocorrelation becomes larger (at a given overall habitat availability). We thus observed the  
7 prevalence of more fat-tailed dispersal kernels due to increased global dispersal in landscapes  
8 characterized by more evenly distributed suitable habitat. The obtained outcome is consistent over  
9 the three different simulation experiments (Fig 2) and does, with exception of a slight decrease in  
10 global dispersal, not depend on the applied submodels for local population dynamics or the  
11 implementation of distance dependent dispersal mortality. Neither did we detect deviations in  
12 scenarios with different  $\lambda$  or  $K$  (results not shown).

13

14 No local adaptation within landscapes was recorded for global dispersal trait values (all  $R^2 < 0.03$ ).  
15 However, local adaptation in the Gaussian component of dispersal emerge when the availability of  
16 habitat  $P$  falls below 0.7 and when at the same time clumping is high ( $H$  within range 0.4-1 (Fig. 3, only  
17 data presented for simple scramble competition). These ranges of landscape structure correspond  
18 with the evolution of local dispersal distances (trait  $G_g$ ) in the range of 1.5-3 units (Fig 2A).

19

20

21

## 1 **Discussion**

2           The availability of habitat and its spatial distribution has a prominent effect on the evolution  
3 of dispersal distances. We show that an increasing proportion of suitable habitat in a landscape  
4 selects – unsurprisingly – for increased dispersal distance, as reflected by the increased investments  
5 into global dispersal and the parallel increase in the local dispersal distances. Yet a change in  
6 autocorrelation inflicts opposing selective pressure on the local and global component of dispersal.  
7 This gives rise to particularly fat-tailed dispersal kernels under conditions of spatially uncorrelated  
8 habitat availability (large fraction of global dispersal but short mean dispersal distance for local  
9 dispersal). Polymorphism in dispersal tactics only emerged in landscapes with low habitat availability  
10 and high spatial autocorrelation and emerged only with respect to the trait coding for the Gaussian  
11 dispersal tactics. This local adaptation emerged in landscapes that select against global dispersal and  
12 for intermediate Gaussian dispersal rates, i.e. in landscapes with less than 70% but strongly clumped  
13 habitat.

14

15           The retrieved patterns are obviously relevant for organisms with mixed dispersal strategies  
16 encompassing (i) more or less controlled short distance dispersal (SDD) and (ii) uncontrolled passive  
17 long distance dispersal (LDD). These conditions hold for seed dimorphic plants with investments for  
18 anemochorous dispersal, insects with facultative wing formation like aphids and some butterflies,  
19 arthropods that use silk as a dispersal mode and probably many organisms that combine passive,  
20 uncontrolled dispersal phases with more active dispersal modes. Neither the implementation of local  
21 logistic growth with contest competition nor the distance dependent dispersal mortality affected this  
22 pattern. Because we implemented asexual reproduction and low local carrying capacities, strong kin  
23 competition can here be attributed to overrule the expected decreasing dispersal under logistic  
24 growth or additional dispersal mortality (Hamilton & May 1977; Ronce et al. 2000; Poethke et al.  
25 2007).

26

27           The few empirical studies that detected a geographic variation in dispersal tactics confirm  
28 our theoretical predictions that (passive) LDD would be advantageous in landscapes with high degrees  
29 of habitat availability (Imbert 2001; Cody & Overton 1996; Bonte et al. 2006, 2007; Cheptou et al.

1 2008), but no evidence for shifts towards more controlled movement methods in highly connective  
2 landscapes were found. To our knowledge, no empirical studies have explicitly tested the relationship  
3 between spatial configuration and the evolution of dispersal polymorphism within heterogeneous  
4 landscapes. However, if we consider detectable movements of butterflies as short distance dispersal  
5 that contrast with probable, but rarely quantified long distance dispersal (Van Dyck & Baguete 2004),  
6 patterns found in a meadow-inhabiting species (Baguette & Schtickzelle 2006) fit our predictions.

7

8           Because our model deals with the evolution of ecological phenomena typical for passively  
9 dispersing organisms, we hypothesised the polymorphism to be adaptive within a landscape if  
10 distances decrease with increased habitat isolation and availability (Bonte et al. 2007; Cheptou et al.  
11 2008). Evidently, different responses can be expected for actively moving organisms with certain  
12 habitat detection abilities (Lima & Zollner 1996). In first instance, our simulations point out the  
13 absence of local adaptation in LDD dispersal strategies. This is not unexpected given the overall low  
14 dispersal rates, rendering the trait more subject to drift than to selection, and the simultaneous gene  
15 flow over very large distances associated with this mode of dispersal. In contrast, local adaptation in  
16 Gaussian dispersal distance was detected in landscapes with high degrees of autocorrelation and  
17 habitat availability up to 70%. These comprise landscapes that on average select for intermediate  
18 dispersal distances and accord with earlier theoretical work on the relationship between gene flow  
19 and local adaptation (Lenormand 2002; Billiard & Lenormand 2005; Garant et al. 2007). Because  
20 dispersal distance is expected to be tightly related to gene-flow, extremely low dispersal distances will  
21 lead to the absence of gene flow and consequently low genetic variation on which natural selection  
22 can act. In contrast, high levels of gene flow through large dispersal distances will be responsible for  
23 gene swamping. High dispersal distances will consequently erode any emergence of local adaptation  
24 in dispersal distance.

25

26           By modelling combined dispersal kernels, we show that different parts of the kernel (i.e.,  
27 SDD and LDD) are affected by different landscape-related selection pressures. Both SDD and LDD  
28 consequently evolve independently, despite the simplicity of the applied simulations. Moreover, it  
29 can be expected that the consideration of (i) different associated dispersal costs and (ii) additional

1 environmental attributes like different rates and spatial extents of disturbance (Muller-Landau et al.  
2 2003) will presumably amplify these independent evolutionary mechanisms.

3

4         Given the relevance of LDD for biological invasions (Muller-Landau et al. 2003) and range  
5 expansion under climate change (Phillips et al. 2008), we can expect serious geographic variation in  
6 range expansion rates for species with distinct dispersal polymorphisms. This geographic variation is  
7 expected to be related to the landscape configuration of source populations with larger range  
8 expansion fronts for those populations, inhabiting landscapes with high levels of naturally or already  
9 long-term fragmented habitat. Evolutionary responses of dispersal kernels at range expansion fronts  
10 are documented (Travis & Dytham 2002, Phillips et al. 2008). Our simulations additionally point out  
11 that the underlying landscape structure should be equally considered when predicting invasive range  
12 expansion of species under global change.

13

#### 14 **Acknowledgements**

15 DB received a mobility grant from the Fund for Scientific Research – Flanders (FWO) for a long-term  
16 stay at Würzburg University. DB was funded by FWO research grant (G.0057.09). HJP and TH are  
17 partially supported by a grant from the “Deutsche Forschungsgemeinschaft” (DFG PO244/4).

18

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- 21

1 Table 1 – Summary of the model parameters

2

Parameter	Description	Ranges tested (sensitivity analysis)
$K$	Carrying capacity local populations	5 (7,10,30*)
$\lambda$	mean offspring number (logistic growth submodel)	2 (3,4,5)
$\mu$	dispersal mortality (distance dependent mortality submodel)	dist/dist <sub>max</sub>
$P$	Proportion of available habitat in the landscape	0.1,0.2,...0.9
$H$	Spatial autocorrelation of the available habitat	0,0.1,0.2,...1

3 \*: analysis done in grid landscape of 128 x 128 cells for computational reasons

4

1 **Figure Legends**

2 **Figure 1 – Examples of fractal landscapes used in simulations. Upper panels contain P=0.2 habitat**  
3 **(black), lower panels P=0.8. Left panels show a more dispersed distribution (H=0.2), right ones are**  
4 **more clumped (H=0.8).**

5

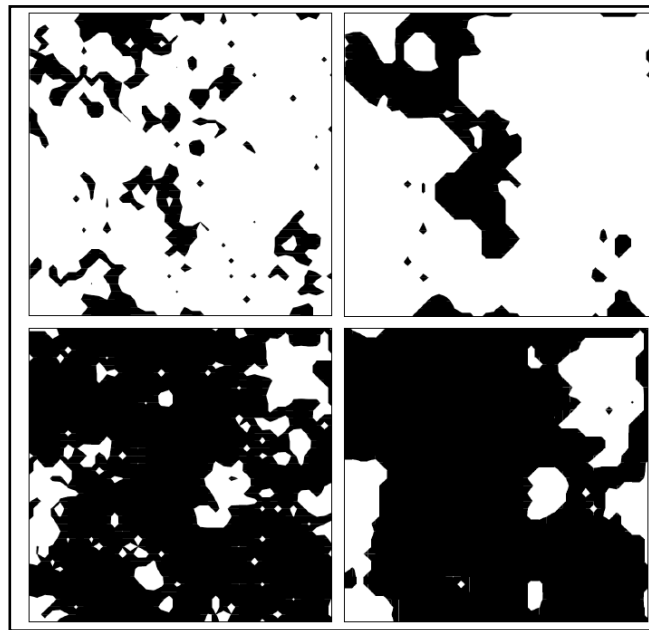
6 **Figure 2 - Mean values for dispersal traits according to the proportion of available habitat (P) and its**  
7 **degree of autocorrelation (H). A,C,E: Mean value of the allele for the Gaussian distance, B,D,F:**  
8 **frequency of individuals performing global dispersal. We present data for respectively the baseline**  
9 **smodel (scramble competition; A,B), logistic growth model (C,D) and baseline model with distance**  
10 **dependent dispersal mortality (E,F).**

11

12 **Figure 3 - A. Strength of local adaptation ( $R^2$ , see material and methods for details) of Gaussian**  
13 **dispersal distance strategies according to the proportion of available habitat (P) and its degree of**  
14 **autocorrelation (H).**

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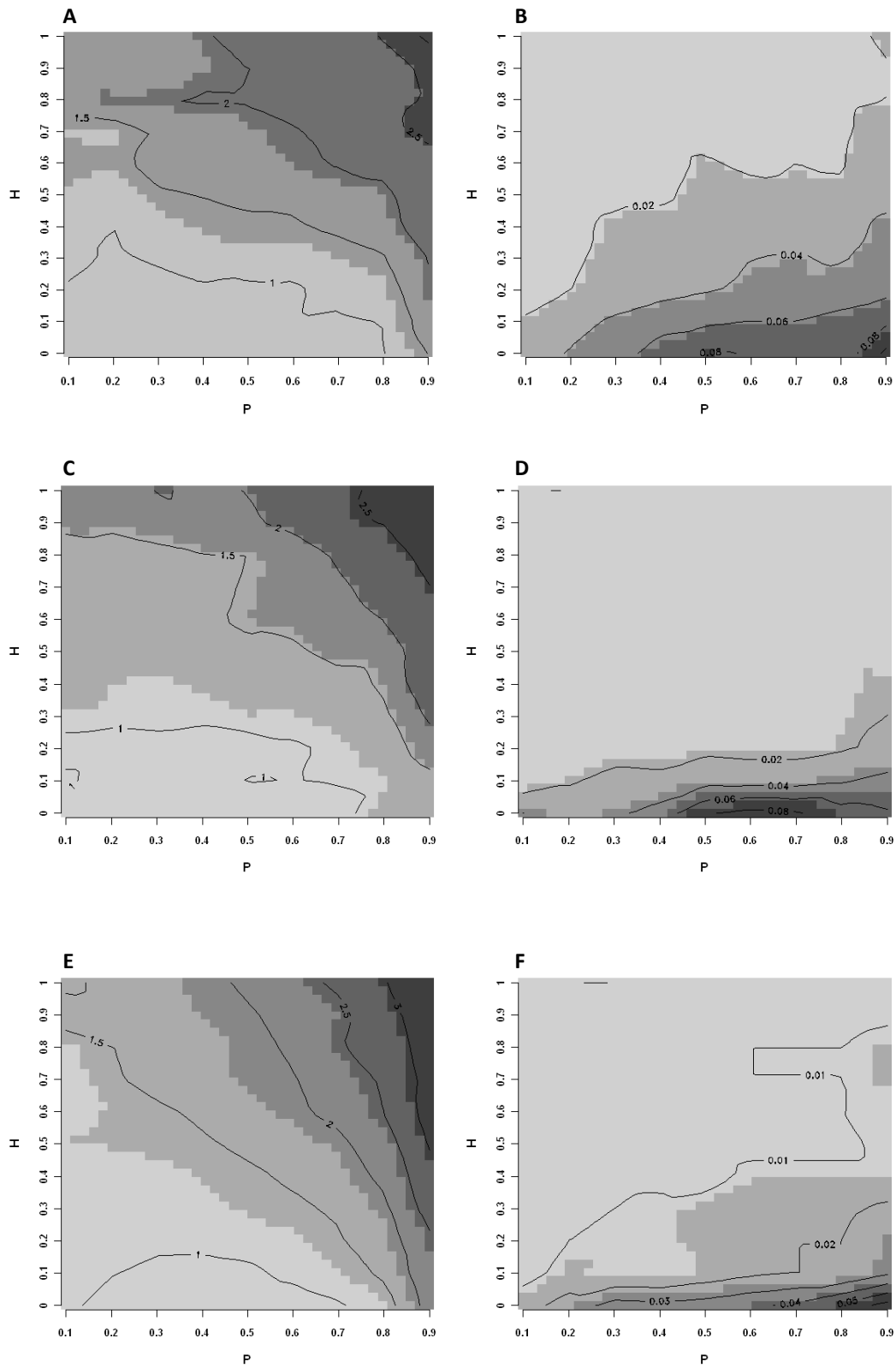
1 **Figure 1 -**



2

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Figure 2 -



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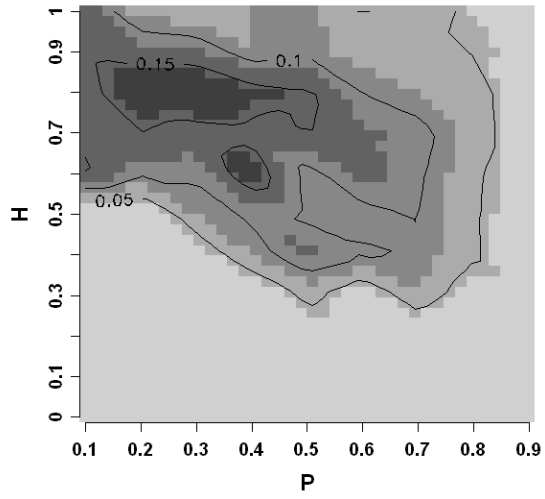
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1 **Figure 3 -**

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