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Joint evolution of specialization and dispersal in structured metapopulations

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Abstract

We study the joint evolution of dispersal and specialization concerning resource usage in a mechanistically underpinned structured discrete-time metapopulation model. We show that dispersal significantly affects the evolution of specialization and that specialization is a key factor that determines the possibility of evolutionary branching in dispersal propensity. Allowing both dispersal propensity and specialization to evolve as a consequence of natural selection is necessary in order to understand the evolutionary dynamics. The joint evolution of dispersal and specialization forms a natural evolutionary path leading to the coexistence of generalists and specialists. We show that in this process, the number of different patch types and the resource distribution are essential.

Key words: Adaptive dynamics, Dispersal, Specialization, Trade-off, Specialist, Generalist, Evolution, Metapopulation

1. Introduction

During the last decades, research has been active both in the field of the evolution of dispersal (see e.g. reviews by Johnson and Gaines (1990); Levin et al. (2003) and Ronce (2007)) and in that of the evolution of specialization (see e.g. reviews by Futuyma and Moreno (1988) and Ravigné et al. (2009)). However, only few studies have focused on the case in which both of the traits can evolve and are subject to natural selection (Kisdi, 2002; Hanski and Heino, 2003; Heinz et al., 2009). The lack of this type of studies has a natural explanation: in order to analyze dispersal, one has to use spatially structured models, which notably complicates the analysis of specialization. Nowadays, the adaptive dynamics approach (Metz et al., 1992; Geritz et al., 1998; Durinx et al., 2008) provides us with tools suitable for a systematic analysis of the course of mutation limited, frequency and density dependent phenotypic evolution, also in the case of spatially structured ecological models (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001; Parvinen, 2006).

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1 Intuitively, one might expect that the interplay between the evolution of
2 dispersal and the evolution of specialization is rather simple: the scarcely dis-
3 persing phenotype should benefit from specialism and adaptation to local con-
4 ditions whereas the amply dispersing phenotype should benefit from generalism
5 and capability to deal with different local conditions. Recent studies in the
6 field of the evolution of specialization have shown, however, that this is not the
7 whole truth. Instead, even non-monotonous relationships seem to be possible
8 (Ronce and Kirkpatrick, 2001; Nurmi et al., 2008; Nurmi and Parvinen, 2008).
9 Therefore it is not possible to fully understand the evolution of specialization
10 without studying the evolution of dispersal.

11 Nurmi and Parvinen (2008) studied the way different ecological factors in
12 a metapopulation affect the evolution of specialization when consumers face a
13 trade-off between the abilities to consume two different resources. We expand
14 their analysis by allowing dispersal to evolve as a consequence of natural selec-
15 tion.

16 In this paper we concentrate on presenting general ideas and results concern-
17 ing the way different ecological factors affect the joint evolution of dispersal and
18 specialization. We do not use any specific real population to estimate parameter
19 values, but instead try to reveal all the significant evolutionary phenomena in
20 the entire biologically realistic parameter domain. Correspondingly, we do not
21 employ any explicit spatial patch configuration, but instead use global migration
22 via a disperser pool. This also allows us to use an explicit algebraic expression
23 for the invasion fitness.

24 Our model applies to several realistic biological systems. For example, sev-
25 eral species of Lepidoptera seek for sodium in a behavior known as puddling.
26 Lepidoptera can use a variety of sodium sources (e.g. mud puddles, dung and
27 carrions), and different species show different patterns of specialization concern-
28 ing the use of resources (Smedley and Eisner, 1995; Boggs and Day, 2004).
29 Naturally, these sources differ in their sodium levels and the amount of energy
30 required to extract a unit of sodium. However, to illuminate the differences
31 between generalists and specialists, we assume that there are two equivalent
32 resources. Our modeling approach readily includes the possible occurrence of
33 energetically different resources, but the inclusion of more than two resources
34 would require a different approach. In the modeling of the population dynamics
35 of Lepidoptera, structured metapopulation models are useful tools, since several
36 Lepidoptera species live in fragmented landscapes in which extinction prone lo-
37 cal populations are connected via dispersal (Harrison and Thomas, 1992). Fur-
38 thermore, our modeling approach enriches the Levins' type metapopulations
39 with explicit resource distributions and dynamics; a step considered necessary
40 for the conservation biology of butterflies by Dennis et al. (2006).

41 Another and more specific example of a biological system that fits the frame-
42 work of our model consist of Glanville Fritillary butterflies (*Melitaea Cinxia*).
43 In Finland, these butterflies have been discovered to use two host plant species
44 and to employ different patterns of specialization concerning the usage of the
45 resources (Hanski and Singer, 2001; Hanski and Heino, 2003).

1 2. The metapopulation model

2 We analyze the same discrete-time model as Nurmi and Parvinen (2008),
3 where

- 4 • The landscape consists of infinitely many spatially distinct habitat patches.
5 Each patch supports a local population and two nutritionally equivalent
6 resources.
- 7 • The local between-season dynamics are mechanistically derived (Geritz
8 and Kisdi, 2004) from a within-season resource–consumer model with the
9 two resources. Deterministic population dynamics consist of clonal repro-
10 duction, emigration, immigration and mortality.
- 11 • Local disasters occur randomly. A disaster wipes out the entire local
12 population but leaves the patch habitable. Catastrophes affect only the
13 consumer populations, not the resources.

14 The mechanistic underpinnings of the metapopulation dynamics enables us to
15 base the analysis of the evolutionary dynamics directly on the individual-level
16 traits (Rueffler et al., 2006). We will next only briefly review the derivation of
17 the metapopulation model. We urge interested readers to consult the articles
18 by Geritz and Kisdi (2004) and by Nurmi and Parvinen (2008) for the details
19 of the derivation.

20 2.1. Mechanistic derivation of the local between-season dynamics

21 The within-season dynamics applies to species that hatch at the beginning
22 of a season, migrate to a new patch with probability e , use local resources to
23 produce eggs that also encounter mortality during the breeding season. At the
24 end of the breeding season, all adults perish and only a fraction of the eggs
25 survives to the following season.

26 In the absence of consumers, continuous-time within-season dynamics of
27 resource i in patch type m are determined by the chemostat dynamics with
28 carrying capacity K_i^m , i.e.,

$$\dot{R}_i^m = \alpha \left(1 - \frac{R_i^m}{K_i^m} \right),$$

29 where R_i^m denotes the density of the resource. One can set parameter α equal to
30 one by scaling the other parameters, see the Appendix by Nurmi and Parvinen
31 (2008) for details. Furthermore, we assume that there is only a finite number
32 of patch types differing from each other only in the carrying capacities of the
33 resources. Consumers differ only in their strategy vectors (e, s) , where $e \in (0, 1]$
34 denotes the probability that an individual decides to emigrate after hatching.
35 An individual survives dispersal with probability π (independent of e). Fur-
36 thermore, $s \in [0, 1]$ stands for the individual's degree of specialization such that
37 $s = 1$ corresponds to a devoted specialist using only resource 1, $s = 0$ to a de-
38 voted specialist using only resource 2, and $s = 0.5$ corresponds to an unbiased

1 generalist. A local population with strategy $e = 0$ (no dispersal) is not viable
 2 since local catastrophes are liable to make this population extinct in the long
 3 run. We assume that mutations may affect only one trait (either specialization
 4 or dispersal) at a time. The two traits can evolve independently, and all kinds
 5 of trait combinations are possible (no pleiotropy). These assumptions allow us
 6 to deduce the qualitative course of evolution using fitness isocline plots (see,
 7 e.g., Figure 1), which is generally not possible for more complicated mutational
 8 variance–covariance structures (Leimar, 2001, 2009).

9 Consumers with strategy (e, s) use type i resource with effort $\beta_i(s)$ according
 10 to the law of mass action. Since the resources are nutritionally equivalent, we
 11 assume that there exists such an increasing function β that $\beta(0) = 0$, $\beta_1(s) =$
 12 $\beta(s)$ and $\beta_2(s) = \beta(1 - s)$. It is possible, by scaling the other parameters
 13 appropriately, to determine (without loss of generality) that $\beta(1) = 1$. Whenever
 14 an explicit definition of the function β is necessary, we define that

$$\beta(s) = \frac{1 - \exp(-\theta s)}{1 - \exp(-\theta)}, \quad \theta \neq 0. \quad (1)$$

15 This formula is not defined for $\theta = 0$, but since $\lim_{\theta \rightarrow 0} \beta(s) = s$, it is natural to
 16 define that $\beta(s) = s$ when $\theta = 0$. The trade-off parameter θ determines whether
 17 the trade-off function (i.e., the resource consumption function) β is concave
 18 ($\theta > 0$), convex ($\theta < 0$) or linear ($\theta = 0$). If it is linear, the trade-off function
 19 $\beta(s) = s$ can be mechanistically interpreted, for example, resulting from search
 20 time allocation between the two resources. In case $\theta \neq 0$, we have not found any
 21 mechanistic explanation for the form of the function β . We simply use negative
 22 values of θ to phenomenologically model the situations with an additional cost
 23 of generalism and positive values of θ to model the situations with an additional
 24 benefit of generalism.

25 Moreover, we assume that there occurs no within-season adult mortality
 26 and that the resource dynamics are fast compared to the consumer population
 27 dynamics, i.e., the resource population is always at the quasi-equilibrium deter-
 28 mined by the consumer population sizes. This allows us to derive the following
 29 Beverton-Holt type fecundity function for a type j consumer who employs strat-
 30 egy (e_j, s_j) and lives in a patch of the type m in a time step n :

$$f^m(s_j, \Phi, X_n) = \frac{\lambda \beta(s_j) K_1^m}{1 + K_1^m \sum_h \beta(s_h) x_n^{(h)}} + \frac{\lambda \beta(1 - s_j) K_2^m}{1 + K_2^m \sum_h \beta(1 - s_h) x_n^{(h)}}, \quad (2)$$

31 where

$$\Phi = \left(\left(\begin{array}{c} e_1 \\ s_1 \end{array} \right), \left(\begin{array}{c} e_2 \\ s_2 \end{array} \right), \dots, \left(\begin{array}{c} e_k \\ s_k \end{array} \right) \right)$$

32 is a vector comprising the strategies employed in the patch and

$$X_n = (x_n^{(1)}, x_n^{(2)}, \dots, x_n^{(k)})$$

33 is a vector comprising the corresponding population sizes in time step n . Pa-
 34 rameter λ determines the intrinsic growth rate of consumers, i.e., how much
 35 eggs can a consumer produce with certain amount of nutrients gained from the
 36 two resources.

1 *2.2. Metapopulation dynamics*

2 The local populations interact only by means of dispersal, which takes place
3 via a common disperser pool. In this process emigrants enter the disperser pool,
4 after which all individuals that survive dispersal are distributed evenly to all
5 patches regardless of their quality or spatial configuration. Let D_n^j to denote the
6 average per patch number of type j dispersers at time step n (disperser pool
7 size of type j dispersers), we can finally determine the actual dynamics of the
8 local population size x_n^j of type j consumers employing strategy (e_j, s_j) in a
9 patch type m in the metapopulation model as

$$x_{n+1}^j = C(n+1)(1 - e_j)f^m(s_j, \Phi, X_n)x_n^j + \pi D_n^j, \quad (3)$$

10 where $C(n+1)$ is a random variable drawn from the Bernoulli distribution with
11 parameter c (catastrophe probability), i.e.,

$$C(n+1) = \begin{cases} 1, & \text{if the local population avoids catastrophes in time step } n \text{ (probability } 1 - c), \\ 0, & \text{if there occurs a local catastrophe after time step } n \text{ (probability } c). \end{cases}$$

12 Note that catastrophes occur between the breeding seasons, and the event
13 of a catastrophe taking place in a specific patch is independent of other patches.
14 When a catastrophe occurs, it wipes out the entire local population (all eggs).
15 In the following season, a new local population is established by immigrants.

16 In principle, we can for each time step calculate D_n^j by summing up the
17 amount of type j disperser produced by each patch $(e_j x_n^j)$. In practice, however,
18 the actual calculation of D_n^j in this way is rather demanding. Fortunately, as
19 we focus only on metapopulations featuring a globally attracting fixed point
20 equilibrium, we can neglect this calculation and solve D_n^j from a fixed point
21 equation. In the fixed point D_n^j has a constant value D^j and this value must be
22 such that once a disperser enters a local population it and its descendants will
23 on average produce exactly one new successful disperser.

24 We can derive an explicit formula for the invasion fitness of a rare mutant in
25 this population model. This derivation follows the guidelines given by Gyllen-
26 berg and Metz (2001) (continuous-time models) and Parvinen (2006) (adaptation
27 to discrete-time models). However, this formula is rather lengthy and thus
28 we prompt the reader to consult Nurmi and Parvinen (2008).

29 We carry out most of the analysis in an environment that is symmetric in a
30 sense that for each patch type with a certain combination of carrying capacities
31 there exists an equally common patch type with swapped carrying capacities.
32 In this case, the unbiased generalist strategy is always a singular specialization
33 strategy, i.e., there is no directional natural selection acting on the specialization
34 component of the strategy. In a symmetric environment, it is easy to point out
35 the differences between generalists and specialists and observe how different
36 ecological factors affect the evolutionary dynamics.

37 **3. Results for one evolving trait**

38 Both the evolution of specialization and the evolution of dispersal obey some
39 rules that are independent of the other component of the strategy vector. To

1 obtain a general overview of the course of the evolution in our model, we first
 2 describe these independent components.

3 *3.1. The evolution of specialization*

4 The results we review here have been presented by Nurmi and Parvinen
 5 (2008). They are valid for any positive dispersal propensity e .

6 In a symmetric environment, the unbiased generalist strategy $s = 0.5$ is
 7 always a singular strategy. The specialist strategies $s = 0$ and $s = 1$ are bound-
 8 aries of the strategy space. Thus the evolutionary uninvasibility coincides with
 9 the evolutionary attractivity.

10 The evolutionary dynamics of specialization are dominated by trade-off pa-
 11 rameter θ , which measures the cost/benefit of generalism (see Equations (1)
 12 and (2)). For low values of θ , the evolutionary dynamics of specialization al-
 13 ways converge to a specialist strategy. As θ increases, the generalist strategy first
 14 turns from an evolutionary repeller into a branching point. Two evolutionarily
 15 repelling non-generalist singular strategies appear, but the specialist strategies
 16 still remain evolutionarily attracting. As θ increases further, the non-generalist
 17 singular strategies diverge further from the generalist strategy and finally leave
 18 the strategy space, after which the evolution of specialization converges to the
 19 generalist strategy independently of the initial state and evolutionary branch-
 20 ing takes place. For even greater values of θ the generalist strategy becomes an
 21 evolutionary endpoint. Nurmi and Parvinen (2008) found no parameter combi-
 22 nations such that both the generalist strategy and the specialist strategies would
 23 appear simultaneously as evolutionary endpoints in a monomorphic population.
 24 Altogether, there are two critical values of θ :

- 25 • At θ_1^* , the generalist strategy turns from an evolutionary repeller into a
 26 branching point.
- 27 • At θ_2^* , the generalist strategy turns from a branching point into an evolu-
 28 tionary endpoint (ESS)

29 According to Nurmi and Parvinen (2008), θ_2^* is for most parameter combinations
 30 located in the neighborhood of zero, which corresponds to linear trade-off.

31 Whenever evolutionary branching occurs ($\theta_1^* < \theta < \theta_2^*$), the population
 32 becomes dimorphic. Usually the evolutionary dynamics of a dimorphic popula-
 33 tion end in the combination of the two extreme specialists $s_1 = 0$ and $s_2 = 1$.
 34 This again is a boundary of the strategy space and thus also an evolutionary
 35 endpoint. However, when θ is only slightly smaller than θ_2^* , the evolutionary
 36 dynamics of a dimorphic population end in a singular strategy pair (s_1, s_2) , in
 37 which $0 < s_1 < 1$ and $s_2 = 1 - s_1$ (in a symmetric environment). Whenever
 38 this singular strategy pair is reached in an evolutionary process starting from a
 39 monomorphic population it is an evolutionary endpoint and further branching
 40 of specialization in the dimorphic population is not possible. We urge inter-
 41 ested readers to consult the article by Nurmi and Parvinen (2008) for further
 42 information.

1 *3.2. The evolution of dispersal*

2 Evolution of dispersal in our model has not been studied previously, but
 3 our findings are qualitatively similar to those by Parvinen (2006) based on a
 4 Ricker-model without specialization. The results we present here are valid for
 5 any specialization strategy s .

6 Trade-off parameter θ dominated the evolution of specialization, whereas it
 7 affects the evolution of dispersal mostly indirectly by setting the evolutionary at-
 8 tractor of the specialization strategy. In a monomorphic population, our model
 9 has only a single evolutionarily singular dispersal propensity, which is always
 10 evolutionarily attracting. The numerical value of this propensity is primarily
 11 determined by catastrophe probability c and probability π of surviving disper-
 12 sal. The higher the probability π , the higher the singular dispersal propensity.
 13 When there remains any risk of dispersal ($\pi < 1$), the catastrophe probabil-
 14 ity affects the singular dispersal propensity in a non-monotonous way: in the
 15 absence of catastrophes ($c = 0$), all local populations stay at the fixed point
 16 of Equation (3) and thus the strategy not to disperse is an evolutionarily at-
 17 tracting singular strategy, as proved by Parvinen (2006). As the catastrophe
 18 probability increases, the singular dispersal propensity increases in the begin-
 19 ning, too. This is due to the fact that catastrophes result in empty patches,
 20 which make dispersal profitable. As the catastrophe probability increases fur-
 21 ther, most individuals find themselves in sparsely populated patches with plenty
 22 of resources. This decreases the advantages of dispersal and causes the singular
 23 dispersal propensity to diminish. The value of the singular dispersal propensity
 24 reaches zero again at the threshold where the metapopulation loses its viability.
 25 This phenomenon has been observed also by, for example Ronce et al. (2000);
 26 Gyllenberg et al. (2002) and Parvinen (2006). In this paper, we focus mainly on
 27 the domain in which the singular dispersal propensity appears as an increasing
 28 function of the catastrophe probability.

29 Various mechanisms resulting in evolutionary branching or polymorphisms of
 30 dispersal have been observed in different metapopulation models. These mech-
 31 anisms include temporal variation in form of cyclic (Doebeli and Ruxton, 1997;
 32 Parvinen, 1999) or chaotic (Holt and McPeck, 1996) local population dynamics,
 33 or temporally and spatially varying carrying capacities (McPeck and Holt, 1992;
 34 Mathias et al., 2001). However, catastrophes alone, have been observed not to
 35 create enough temporal variation to promote branching. For example, Gyllen-
 36 berg et al. (2002) did not find evolutionary branching in a structured metapop-
 37 ulation model defined in continuous time with one patch type. Parvinen (2002)
 38 studied the corresponding model with several patch types, and observed that
 39 catastrophes together with spatial heterogeneity in the sense of different patch
 40 types can result in evolutionary branching of dispersal. The necessary level
 41 of spatial heterogeneity can be obtained with differences in growth conditions
 42 alone, as well as with differences in catastrophe rates alone. A similar observa-
 43 tion in a metapopulation model with small local populations, and thus locally
 44 stochastic population dynamics, was made by Parvinen et al. (2003) (one patch
 45 type) and Parvinen and Metz (2008) (several patch types).

1 Parvinen (2006) studied a discrete-time metapopulation model and found
 2 another additional mechanism, which can together with catastrophes result in
 3 evolutionary branching. Even though all local populations would eventually
 4 reach an equilibrium population size, if they are not hit by a catastrophe, this
 5 convergence to the equilibrium can be non-monotonous due to overcompensation
 6 in the local discrete-time dynamics, such as in the Ricker model. Parvinen
 7 (2006) observed that such temporal heterogeneity together with catastrophes
 8 can result in evolutionary branching of dispersal.

9 Local growth in the metapopulation model studied in this article is of the
 10 Beverton-Holt type, where convergence to the population-dynamical equilibrium
 11 is monotonous. Therefore the mechanism for evolutionary branching of dispersal
 12 observed by Parvinen (2006) is not present here. According to our observations,
 13 the evolutionarily singular dispersal propensity is in most cases uninvadable by
 14 mutants featuring a different dispersal propensity. As can be expected based
 15 on the reasoning above, we can observe evolutionary branching of dispersal, if
 16 individuals encounter a sufficient amount of spatial heterogeneity in the sense
 17 of different patch types (Parvinen, 2002). An unbiased generalist regards the
 18 two resources as identical and therefore it observes no difference between two
 19 patches with swapped resource carrying capacities ($K_1^1 = K_2^2$ and $K_2^1 = K_1^2$).
 20 The reasoning above together with our numerical results let us conjecture that
 21 evolutionary branching of dispersal is not possible in a metapopulation com-
 22 prising unbiased generalist individuals in an environment comprising two patch
 23 types with swapped carrying capacities. For a specialist, evolutionary branching
 24 of dispersal in such an environment is possible (Figures 1B and 3B).

25 **4. Joint adaptive dynamics of specialization and dispersal**

26 *4.1. Evolutionary scenarios in a symmetric environment comprising two patch* 27 *types*

28 In this section, we analyze the case in which both of the aforementioned
 29 traits can evolve and are subject to natural selection.

30 As mentioned above, we are able to derive an explicit algebraic formula for
 31 the fitness function of the model. We have not found means for mathematical
 32 analysis of this formula. Instead, all our results concerning the evolution of a
 33 monomorphic population rely on numerical analysis of this formula. We illus-
 34 trate the course of evolution by showing the fitness gradient isoclines of dispersal
 35 and specialization: we plot the evolutionarily singular dispersal propensities as
 36 a function of the specialization strategy on the vertical axis together with the
 37 singular specialization strategies as a function of the dispersal propensity on
 38 the horizontal axis. From these isocline plots, we deduce the way dispersal and
 39 specialization evolve in a monomorphic population.

40 Although it is, in principle, possible to solve polymorphic singular strategies
 41 numerically, it is more illustrative to follow the course of the evolution starting
 42 from a monomorphic population. The expected course of evolution in the case in
 43 which mutations would be infinitesimally small could be analyzed by using the

1 canonical equation of adaptive dynamics (Dieckmann and Law, 1996). In this
 2 paper, however, we illustrate evolution in a polymorphic population by using
 3 evolutionary simulations that include the effects of mutational stochasticity (see
 4 Appendix).

5 From the evolutionary simulations, we can deduce the evolutionary end-
 6 points, and use the speed at which the evolution of dispersal and specialization
 7 proceeds to compare the strengths of the evolutionary forces influencing these
 8 traits. This is possible, because we run our simulations with identical evolution-
 9 ary parameters (mutation rate, expected size and variance of the mutations etc.)
 10 for dispersal and specialization. The simulations we present are not individual
 11 based, instead, they result from repeated iterations of the metapopulation dy-
 12 namics and infrequent insertions of new mutants employing a strategy close to
 13 one of the resident strategies. See Appendix for the description of the simula-
 14 tion procedure. The evolutionary time on the horizontal axis of the simulation
 15 figures is an abstract concept only applicable to comparison between the times
 16 that are needed to obtain different evolutionary endpoints.

17 Figures 1 and 2 illustrate the qualitatively different fitness gradient isocline
 18 configurations that are possible in symmetric environments. Figure 1 illustrates
 19 all qualitatively different isocline configurations possible in environments com-
 20 prising two patch types with swapped carrying capacities. Besides the case with
 21 swapped carrying capacities, an environment is symmetric also when within each
 22 patch type the carrying capacities of the two resources are equivalent although
 23 they differ between patch types. Furthermore, in environments comprising more
 24 than two patch types there are several ways to construct symmetric environ-
 25 ments. Isocline configurations in such environments are illustrated in Figure 2
 26 to the extent that they are qualitatively different from those in Figure 1.

27 In each column in Figure 1 the value of the parameter θ increases from
 28 top to down, while other parameters are kept constant. This illustrates the
 29 bifurcation pattern depicted in section 3.1 for the evolutionary dynamics of
 30 specialization. The panels with $\theta = -3$ (strong trade-off and strongly convex
 31 trade-off function), $\theta = -1$ (moderately strong trade-off and weakly convex
 32 trade-off function), and $\theta = 1$ (weak trade-off and concave trade-off function)
 33 illustrate the evolutionary scenarios that are "typical" in the model, whereas
 34 the evolutionary phenomena depicted in panels with $\theta = -1.8$ and $\theta = 0.1$
 35 take place only in narrow intermediate parameter domains. The results of the
 36 evolutionary simulations corresponding to these "typical" cases are collected to
 37 Figure 3.

38 Figures 1A, 3A, 1B, and 3B illustrate the case with strong trade-off (high
 39 cost of generalism). There the specialization strategy first evolves to full spe-
 40 cialism ($s = 0$ or $s = 1$, depending on the initial state). In the case illustrated
 41 in Figures 1A and 3A evolutionary dynamics end in a monomorphic specialist
 42 population. If dispersal survival π is sufficiently high, evolutionary branching
 43 of dispersal may occur (Figures 1B and 3B). Branching results in a dispersal di-
 44 morphism where two morphs can coexist in a metapopulation because the more
 45 dispersive morph is able to occupy empty patches efficiently but is outcompeted
 46 locally by the less dispersive morph in the case the patch avoids catastrophes suf-

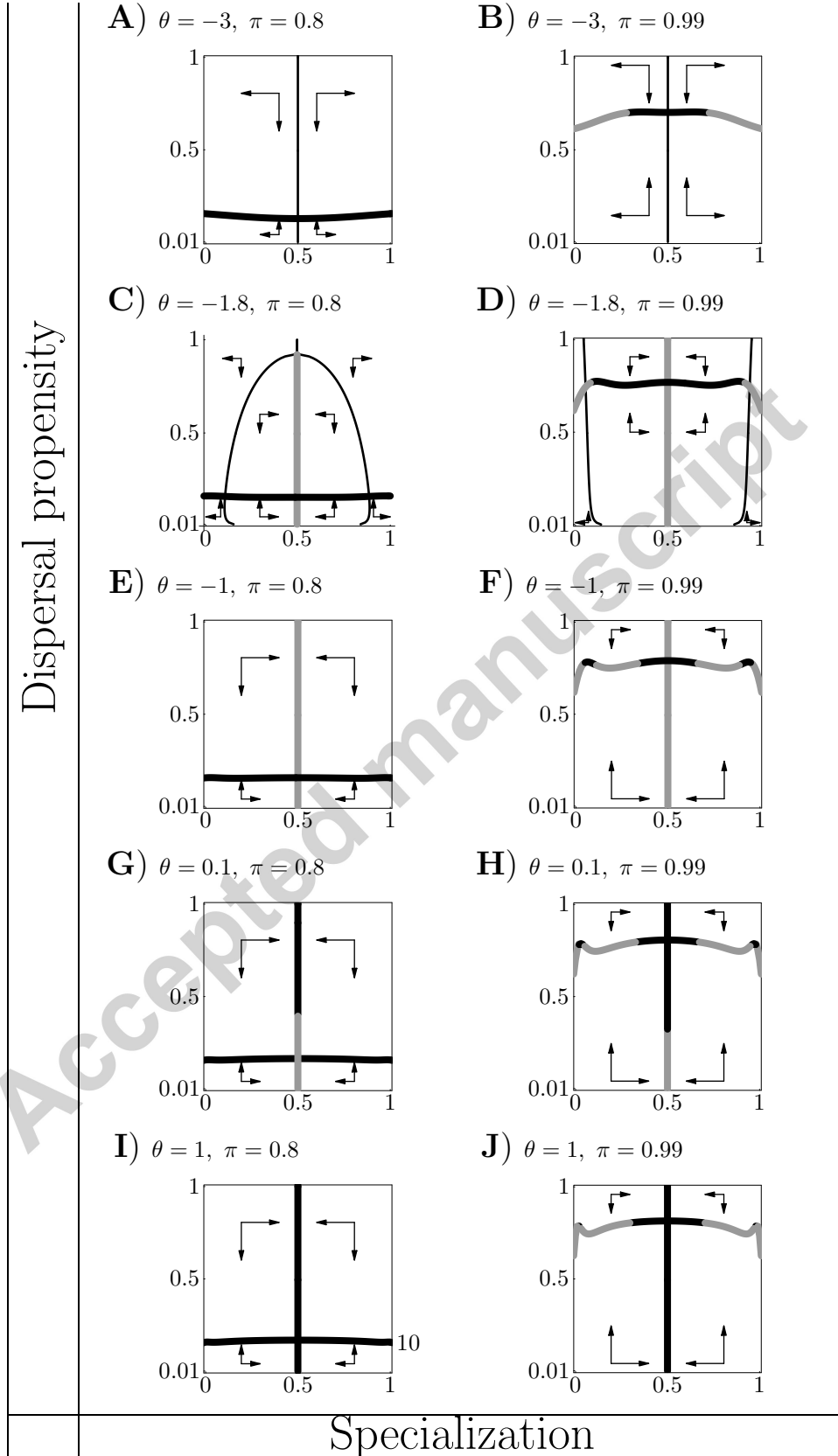


Figure 1: **Symmetric environments comprising two patch types with swapped carrying capacities:** Evolutionarily singular specialization strategies as a function of dispersal propensity (horizontal axis) and singular dispersal propensities as a function of specialization (vertical axis). Thick black curve = CSS, thick grey curve = branching point, thin black curve = evolutionary repeller. Parameter values: $\lambda = 3$, $c = 0.05$, $K_1^1 = K_2^2 = 3$, $K_1^2 = K_2^1 = 1$ and $p_1 = p_2 = 0.5$

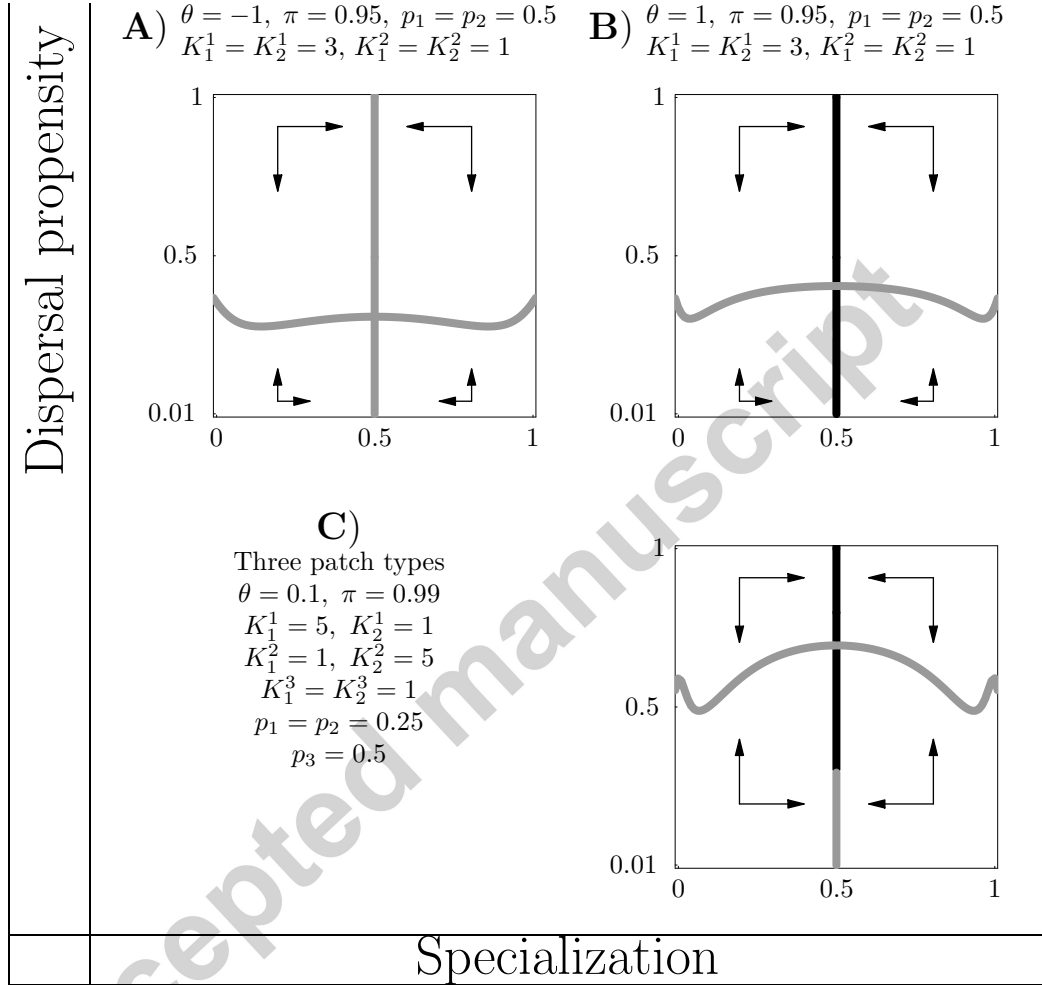


Figure 2: **Symmetric environments II:** Evolutionarily singular specialization strategies as a function of the dispersal propensity (horizontal axis) and the singular dispersal propensity as a function of specialization (vertical axis). Thick black curve = CSS, thick grey curve = branching point, thin black curve = evolutionary repeller. Parameter values: $\lambda = 3, c = 0.05$

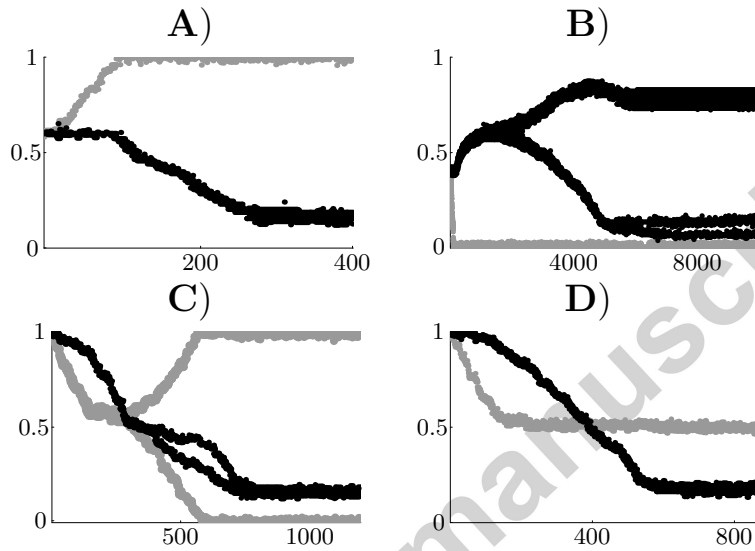


Figure 3: Strategies present in the metapopulation during an evolutionary simulation. Grey curve: the specialization component s of the strategy, black curve: the dispersal component e . Initial strategies A: $(e, s) = (0.6, 0.6)$, B: $(e, s) = (0.4, 0.4)$, C and D: $(e, s) = (1, 1)$. Parameter values in panels A, B, C and D correspond to the ones in Figure 1A, 1B, 1E and 1I, respectively. The simulation ends up in
A: a monomorphic population using strategy $(e, s) \approx (0.15, 1)$.
B: a dimorphic population using strategies $(e, s) \approx (0.1, 0)$ and $(0.7, 0)$.
C: a dimorphic population using strategies $(e, s) \approx (0.15, 1)$ and $(0.15, 0)$.
D: a monomorphic population using strategy $(e, s) \approx (0.18, 0.5)$.

1 ficiently long. In the case illustrated Figures 1B and 3B consumers utilize solely
 2 one resource leaving the other intact. The other resource is, however, capa-
 3 ble of sustaining a corresponding dispersal dimorphism; Figure 4 illustrates, for
 4 slightly different parameter values, the way evolutionary branching of special-
 5 ization initiates an evolutionary path that leads to a quadrimorphic population
 6 comprised of two differently specialized dispersal dimorphisms.

7 Figures 1I, 1J, and 3D illustrate the case with weak trade-off (additional ben-
 8 efit of generalism). In this case the evolutionary dynamics of specialization end
 9 in a monomorphic generalist population and evolutionary branching of dispersal
 10 is not possible (see section 3.2). An evolutionary simulation corresponding to
 11 the isocline configuration depicted in Figure 1I is illustrated in Figure 3D. An
 12 evolutionary simulation corresponding to the isocline configuration depicted in
 13 Figure 1J would be qualitatively similar (not illustrated).

14 Figures 1E, 1F, 3C, and 4 illustrate the case with moderately strong trade-
 15 off. There a monomorphic population first evolves to generalism, and then
 16 evolutionary branching of specialization occurs resulting in a metapopulation
 17 comprising two devoted specialists. Due to the symmetry of the environment,
 18 the two specialist morphs encounter identical selective forces influencing dis-
 19 persal propensity and thus the dispersal propensities end up in equal values.
 20 However, since mutations occur randomly, the evolutionary paths in the strat-
 21 egy space are not identical. In the case illustrated in Figures 1E and 3C dis-
 22 persal is rather risky ($\pi = 0.8$) and evolutionary branching of dispersal is not
 23 possible. Thus, finally evolutionary dynamics end in a dimorphic population
 24 comprising two scarcely dispersing devoted specialists. If dispersal survival is
 25 high ($\pi = 0.99$), as is the case in Figures 1F and 4, evolutionary branching of
 26 dispersal may follow that of specialization. The evolutionary dynamics end in
 27 a quadrimorphic metapopulation, where each of the two resources hosts both
 28 scarcely and moderately dispersing specialists.

29 Figures 1C and 1D illustrate cases where there may appear several evolu-
 30 tionarily singular specialization strategies and, depending on the initial strategy,
 31 the evolution of specialization in a monomorphic population may proceed either
 32 to generalism or specialism. However, since we now study the evolution of a
 33 two-dimensional strategy, the initial state no longer solely determines the fate
 34 of the population: Figure 5 shows the results of two evolutionary simulations
 35 with one and the same initial state and ecological and evolutionary parameters
 36 (corresponding to Figure 1C). The initial strategy lies in the strategy domain
 37 where the evolution of specialization directs towards specialism. The result
 38 of an evolutionary simulation leading to a monomorphic specialist population
 39 is shown in Figure 5A. However, mutations affect randomly either specialism
 40 or dispersal. It thus is possible that by coincidence or due to the work of a
 41 "Darwinian Demon" (in a sense of Leimar (2001)), a long sequence of succes-
 42 sive mutations affects only dispersal propensity. This is the case in the initial
 43 phase of the simulation illustrated in Figure 5B, where dispersal propensity di-
 44 minishes while specialization remains unchanged in the absence of mutations
 45 affecting specialization. As a result, the prevailing strategy of the metapop-
 46 ulation is such that the specialization strategy is in the neighborhood of the

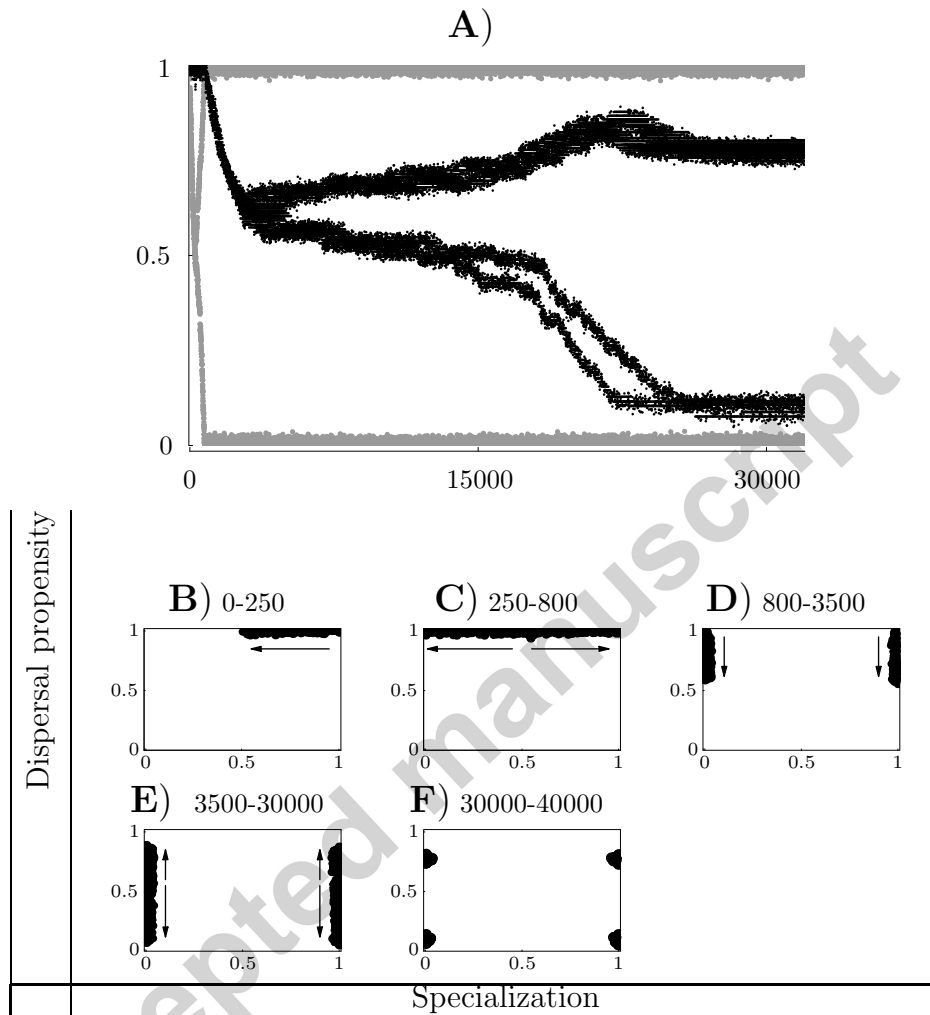


Figure 4: Panel A illustrates strategies present in the metapopulation during an evolutionary simulation. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e . Each dot in Panels B-F represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s . The arrows in Panels B-F indicate the direction of evolution. The initial strategy $(e, s) = (1, 1)$. The simulation ends up in a quadrimorphic population using strategies $(e, s) \approx (0.1, 0)$, $(0.1, 1)$, $(0.8, 0)$ and $(0.8, 1)$. Parameter values correspond to the ones in Figure 1F.

1 repelling singular specialization strategy that is not an ESS. (See, e.g., Figure
 2 2 of Nurmi and Parvinen (2008), top row, case $\theta = -1.2$). In the neighbor-
 3 hood of such a singular strategy there are typically strategies that can coexist
 4 (Case (a) in Figure 2 of Geritz et al. (1998)). As illustrated in Figure 4 of Geritz
 5 et al. (1998), dimorphic selection near a non-ESS singular strategy is disruptive.
 6 Therefore, evolutionary branching of specialization will occur, and finally evo-
 7 lutionary dynamics end in a dimorphic population with two specialist strategies
 8 as illustrated in Figure 5B. Note that when the strategy is one-dimensional we
 9 never observe evolutionary branching near a repelling non-ESS singular strat-
 10 egy, because the evolution of a monomorphic population does never enter the
 11 neighborhood of such a singular strategy. The evolutionary simulation corre-
 12 sponding to the isocline configuration depicted in Figure 1D is not illustrated
 13 here since it is qualitatively similar to the one in Figure 5, expect that instead
 14 low dispersal propensities evolutionary dynamics end in dispersal dimorphisms.
 15 Thus the observed evolutionary endpoint is either qualitatively similar to the
 16 one in Figure 3B or to the one in Figure 4.

17 Figure 1G depicts the fitness gradient isocline configuration in the case with
 18 moderately concave trade-off function (small benefit of generalism). The iso-
 19 cline configuration looks rather simple, whereas the result of a corresponding
 20 evolutionary simulation shown in Figure 6 is surprisingly complicated. The
 21 simulation illustrates how decreasing dispersal propensity triggers evolutionary
 22 branching of specialization. However, the divergent forces caused by the ten-
 23 dency to reduce competition are, in this ecological setting, not strong enough
 24 to override the benefits of generalism, and specialization approaches an inter-
 25 mediate singular strategy pair instead of a full specialization.

26 The two specialization strategies are, however, specialized enough to enable
 27 evolutionary branching of dispersal. In Figure 6E both traits appear to undergo
 28 simultaneous evolutionary branching. However, the driving force underlying this
 29 phenomena is evolutionary branching of dispersal. The changes in the dispersal
 30 propensity of a certain morph also change the evolutionary forces acting on
 31 the specialization strategy of the morph. The evolutionary forces acting on
 32 specialization are in this setting strong enough to cause detectable changes in
 33 specialization already while evolutionary branching of dispersal is underway.

34 Once evolutionary branching of dispersal has occurred, the more dispersive
 35 morphs start to evolve towards generalism while the less dispersive morphs
 36 become more specialized. Finally, either both of the more dispersive morphs
 37 converge to generalism or one of them dies out and the other converges to
 38 generalism (see Figure 6). This results in a trimorphic coexistence of a generalist
 39 and two specialists. In this trimorphism the more dispersive morph finds its
 40 niche by efficiently colonizing patches emptied by catastrophes. On the other
 41 hand, the low dispersal specialists get along as, in the long run, they can take
 42 over the patches rich in the resource they are specialized in.

43 Usually higher dispersal survival results in larger parameter domain where
 44 evolutionary branching of dispersal is possible. Surprisingly, in the case with
 45 $\theta = 0.1$ (Figures 1G and 1H) the effect is opposite. In the case illustrated in
 46 Figure 1H with $\pi = 0.99$ a monomorphic generalist population results whereas

1 in the case illustrated in Figure 1G with $\pi = 0.8$ evolutionary dynamics end
 2 in a trimorphic population. The evolutionary simulation corresponding to the
 3 isocline configuration 1H is not illustrated here since it is qualitatively similar
 4 to the one in Figure 3D.

5 However, the phenomenon depicted in Figure 6 occurs only in a narrow inter-
 6 mediate parameter domain: for most parameter combinations, evolutionary
 7 branching of dispersal is not possible in a metapopulation consisting of inter-
 8 mediately specialized individuals. Furthermore, it requires fine-tuning of the
 9 parameter values to obtain evolution to a dimorphic metapopulation featuring
 10 two intermediately specialized morphs. To sum up, in symmetric environments
 11 with two patch types evolution to the coexistence of generalists and specialists
 12 is an extremely rare occasion. However, when there are more than two patch
 13 types the situation is different.

14 Besides the case with swapped carrying capacities, an environment is sym-
 15 metric also when within each patch type the carrying capacities of the two
 16 resources are equivalent although they differ between patch types. In this case
 17 dispersal does not affect the invadability of the unbiased generalist strategy and
 18 hence only rather simple evolutionary scenarios are possible. A simple calcula-
 19 tion shows that if the trade-off function is concave ($\theta > \theta_2^* = 0$), the evolutionary
 20 dynamics of specialization always end in generalism. If the trade-off function
 21 is convex ($\theta < \theta_2^* = 0$) the evolutionary dynamics of specialization always end
 22 either in the combination of two specialists or in a monomorphic specialist pop-
 23 ulation. Evolutionary branching of dispersal is, in this setting, possible both
 24 in metapopulations consisting of specialists and in metapopulations consisting
 25 of generalists if there are sufficiently different patch types and sufficiently high
 26 dispersal survival (π). Compared with Figure 1, the only qualitatively different
 27 evolutionary scenarios are those involving evolutionary branching of dispersal
 28 in a metapopulation comprising generalists. Panels A and B in Figure 2 illus-
 29 trate the fitness isocline configurations in these cases and Figure 7 illustrates
 30 the results of the corresponding evolutionary simulations.

31 Figures 2A and 7A illustrate the case in which evolutionary dynamics end in
 32 a dispersal dimorphism in a metapopulation consisting of generalist individuals.
 33 Figures 2B and 7B illustrate the case in which the evolution of a monomorphic
 34 population converges to a generalist strategy that is a branching point both for
 35 the specialization strategy and for the dispersal propensity. In this case the
 36 evolutionary endpoint is qualitatively similar to the one in Figure 4.

37 In Figure 2C, the environment is symmetric and comprises three patch types.
 38 Section 4.2 below is devoted to the detailed analysis of this case, where it is pos-
 39 sible that after evolutionary branching of dispersal, only the scarcely dispersing
 40 morph undergoes evolutionary branching of specialization and finally the evo-
 41 lutionary dynamics end in a combination of two scarcely dispersing specialists
 42 and an abundantly dispersing generalist.

1 *4.2. Qualitatively different evolutionary scenarios in symmetric environments*
 2 *comprising more than two patch types*

3 Mostly, our results with two patch types are qualitatively similar to those
 4 with several different patch types. The only essential qualitative difference is
 5 the following: In a symmetric environment with two patch types either evo-
 6 lutionary branching of dispersal is not possible in a metapopulation consist-
 7 ing of generalists (environments with swapped resource carrying capacities) or
 8 dispersal propensity does not affect the invadability of the generalist strategy
 9 (environments where the resource carrying capacities are equal in each patch
 10 type). In an environment with more than two patch types it is easy to find
 11 such parameter combinations that branching of dispersal propensity is possible
 12 in a metapopulation comprising generalists, and that the dispersal propensity
 13 significantly affects the invadability of the generalist strategy.

14 This provides a natural evolutionary path to the coexistence of generalists
 15 and specialists: After the initial phase of evolutionary branching of dispersal,
 16 the two branches diverge further apart from each other and, given that trade-off
 17 parameter θ has an appropriate value, the generalist strategy may turn from
 18 an ESS to an evolutionary branching point for the less dispersive morph. This
 19 results in evolutionary branching of the specialization strategy employed by
 20 the scarcely dispersing morph. In environments comprising two patch types,
 21 evolution hardly leads to the coexistence of specialists and generalists and can
 22 only be observed in a narrow parameter domain. In symmetric environments
 23 comprising several patch types it is easy to construct parameter combinations
 24 where the evolutionary dynamics of an initially monomorphic population end
 25 in the coexistence of two specialists and a generalist, as illustrated in Figures
 26 2C and 8.

27 Note that although panel A in Figure 8 may seem to indicate a degenerate
 28 case in which specialization divides in three branches, this is not the case. In-
 29 stead, after evolutionary branching of dispersal, both morphs employ the same
 30 specialization strategy, $s = 0.5$. The morph with low dispersal propensity un-
 31 dergoes branching of specialization into two branches, while the specialization
 32 strategy of the high-dispersal morph remains at $s = 0.5$ as illustrated in Figures
 33 8B-F.

34 In our model, each evolutionary path to the trimorphic coexistence of two
 35 specialists and a generalist involves evolutionary branching of dispersal in a
 36 metapopulation comprising generalist or nearly generalist individuals. There-
 37 fore, it is of interest to study when evolutionary branching of dispersal is possi-
 38 ble. Figure 9 illustrates the way dispersal survival π , catastrophe probability c
 39 and the distribution of the resources in the environment affect the possibility of
 40 evolutionary branching of dispersal in metapopulations consisting of generalist
 41 individuals.

42 Evolutionary branching of dispersal in a metapopulation consisting of gen-
 43 eralists does not alone ensure evolution to the coexistence of specialists and
 44 generalists. In addition, trade-off parameter θ must have an appropriate value
 45 (according to our observations usually in the neighborhood of $\theta = 0.1$) and the

1 resource distribution must be such that dispersal affects the benefits of special-
 2 ization. To sum up, Figure 9 does not illustrate the parameter domain where
 3 evolution dynamics end in the coexistence of generalists and specialists, but
 4 gives a rough approximation of the parameter domain where such evolutionary
 5 scenarios may be found.

6 In Figure 9 each curve corresponds to a different resource distribution. The
 7 singular dispersal propensity is a branching point above the curves and an ESS
 8 below. Based on Figure 9, one can observe that the size of the parameter domain
 9 where branching may occur is mainly determined by the difference between
 10 patches that act as sources and "pseudo-sinks" in the metapopulation dynamics
 11 (Watkinson and Sutherland, 1995) whereas the fraction of source patches or
 12 total resource availability (column K^*) only have a small effect.

13 4.3. Qualitatively different evolutionary scenarios in asymmetric environments

14 Although assuming a symmetric environment simplifies the analysis of evo-
 15 lutionary dynamics, since the unbiased generalist strategy $s = 0.5$ is then evo-
 16 lutionary singular, it is not biologically very realistic. However, for most asym-
 17 metric environments without a strong bias in the total metapopulation level
 18 amounts of resources, there still exists a unique singular specialization strat-
 19 egy and the evolutionary dynamics are qualitatively similar to a case with a
 20 symmetric environment.

21 The previously analyzed case with two patch types and swapped carrying
 22 capacities becomes asymmetric, when the proportions of the two patch types
 23 are not equal. Figures 10A-D illustrate qualitatively different evolutionary sce-
 24 narios in this case. Note that an unbiased generalist with strategy $s = 0.5$ still
 25 observes no differences between the two patch types, and thus the evolution-
 26 ary singular dispersal propensity is not a branching point for $s \approx 0.5$. Another
 27 option to break the symmetry is to use non-swapped carrying capacities. Re-
 28 sources may be on average equally common throughout the metapopulation, but
 29 are distributed unevenly to patches (Figure 10E and F). In this case a source-
 30 (pseudo-)sink structure (Watkinson and Sutherland, 1995) is possible for the
 31 dynamics of metapopulation consisting of generalists, and the evolutionary sin-
 32 gular dispersal propensity may be a branching point for $s \approx 0.5$.

33 Panel A of Figure 10 shows that when the singular specialization strategy is
 34 evolutionarily repelling, it becomes biased towards the less abundant resource
 35 (as expected). This entails that the more abundant the resource is, the larger is
 36 the basin of attraction of the evolutionary dynamics of the corresponding spe-
 37 cialist strategy. On the other hand, Panels B and C of Figure 10 show that, when
 38 the singular strategy is evolutionarily attracting, it is biased towards the more
 39 abundant resource. However, when the absolute value of the trade-off param-
 40 eter θ becomes sufficiently high, the additional costs or benefits of generalism
 41 overwhelm the effects of asymmetry and the singular specialization strategy
 42 remains close to the unbiased generalist strategy. More detailed analyses of the
 43 evolution of specialization in asymmetric environments have been presented by
 44 Nurmi and Parvinen (2008) and Parvinen and Egas (2004) (featuring a constant
 45 dispersal propensity).

1 Figure 10D illustrates the case in which the singular specialization strategy
 2 is sufficiently distant from the unbiased generalist strategy $s = 0.5$ in order
 3 to enable evolutionary branching of dispersal. The result of a corresponding
 4 evolutionary simulation is shown in Figure 11. We actually observe two suc-
 5 cessive events of evolutionary branching of dispersal. In both cases the disper-
 6 sal propensity at the branching point is rather large. Therefore the dispersal
 7 propensity of one of the emerging morphs cannot increase much more and it
 8 remains nearly generalist, while the dispersal propensity of the other emerging
 9 morph decreases substantially. During the first event of evolutionary branching
 10 the morph with decreasing dispersal propensity specializes in the less abundant
 11 resource 1 ($s = 1$), whereas during the second evolutionary branching the newly
 12 appeared morph with decreasing dispersal propensity specializes in the more
 13 abundant resource ($s = 0$). Finally, the metapopulation reaches a trimorphic
 14 state comprised of one abundantly dispersing generalist and two scarcely dis-
 15 persing specialists. The exploited niches are qualitatively similar to those in the
 16 case involving symmetric environments (Figure 6).

17 Figures 10E and 10F illustrate the cases with non-swapped carrying ca-
 18 pacities, where each resource is in total equally abundant. The evolutionary
 19 simulation illustrated in Figure 12 (corresponding to Figure 10E) ends in a
 20 combination of the two devoted specialists such that one specialist undergoes
 21 evolutionary branching of dispersal whereas the other converges to a single dis-
 22 persal propensity (Compare with Figure 4).

23 The fitness isocline configuration illustrated in Figure 10F resembles the one
 24 illustrated in Figure 2C (with three patch types) and hence one might intuitively
 25 expect that evolution to the trimorphic coexistence of a generalist and two
 26 specialists could be possible also in a two-patch environment with non-swapped
 27 carrying capacities. However, we have not found any parameter combinations
 28 resulting in such a scenario. Instead, evolutionary dynamics typically end in
 29 a dimorphic population comprising one amply dispersing generalist and one
 30 scarcely dispersing specialist as illustrated in Figure 13.

31 *4.4. Evolutionary effects of the parameters that determine the ecological dynam-* 32 *ics*

33 In this section we analyze the way the parameters that determine the eco-
 34 logical dynamics affect the evolutionary dynamics. We carry out our analysis
 35 in a symmetric environment comprising two patch types with swapped carrying
 36 capacities, but we believe that our results are fairly robust against moderate
 37 changes in the structure of the environment.

38 Even though small changes in the trade-off parameter θ usually do not have
 39 direct significant effects on the evolution of dispersal, θ is an essential element
 40 in the evolution of dispersal because of indirect effects. It namely determines
 41 the concavity or convexity of the trade-off function $\beta(s)$ and thus has a signif-
 42 icant effect on the evolutionary attractors in which the evolutionary dynamics
 43 of specialization end in. Figure 14 illustrates the dispersal propensity at the
 44 evolutionary endpoint(s) as a function of the trade-off parameter θ . Evolu-

1 tionary branching of dispersal is not possible in the parameter domain under
2 consideration.

3 Since the two resources are nutritionally equivalent and the environment
4 is symmetric in Figure 14, the specialists employing strategy $s = 0$ encounter
5 equivalent environmental conditions as the specialists using strategy $s = 1$.
6 Thus the evolutionary forces influencing dispersal are similar and, therefore, we
7 observe only one manifestation of evolutionarily singular dispersal propensity
8 even when the population is dimorphic and includes the two specialists (Figure
9 14, areas B and C). Furthermore, since $\beta(0) = 0$ and $\beta(1) = 1$ are independent of
10 θ , the trade-off parameter cannot affect the ecological dynamics or the evolution
11 of dispersal as long as the metapopulation comprises only devoted specialists
12 (the values of θ sufficiently small). Moreover, devoted specialists utilize only the
13 resource they are specialized in and do not affect the availabilities of the other
14 resource to any extent. This means that specialists using strategy $s = 0$ do
15 not affect the ecological dynamics of the specialists employing strategy $s = 1$.
16 Altogether, the evolution of dispersal invariably occurs under similar conditions
17 both in a monomorphic population comprised of devoted specialists using either
18 strategy $s = 0$ or strategy $s = 1$ and in a dimorphic population comprised of
19 the two specialists. Therefore we observe a straight line across areas A, B, and
20 C in Figure 14.

21 The sizes of the local specialist populations are greatest in the patches where
22 the specialists are well-adapted. Since, in our model, dispersal is undirected,
23 the dispersing specialists usually have a rather high risk of ending up in a patch
24 that is less favorable than the original patch. Thus it is natural that the singular
25 dispersal propensity is greatest in area D of Figure 14, where the metapopulation
26 consists of unbiased generalists employing strategy $s = 0.5$. Furthermore, the
27 singular dispersal propensity appears in area D as an increasing function of θ .
28 This is natural since, for generalists, increasing θ results in an increased value
29 for the resource usage effort β for both resources. This increases fecundity and
30 speeds up the population growth especially in small local populations which,
31 again, makes dispersal more profitable (see equations (1) and (2)).

32 Since the trade-off parameter θ measures the additional benefit or cost of
33 generalism, one can use the information on the way different parameters affect
34 the critical values θ_1^* and θ_2^* to deduce the way changes in different parame-
35 ters affect the evolutionary capabilities of the different specialization strategies.
36 Nurmi and Parvinen (2008) have shown that, when dispersal propensity has a
37 constant value, factors that favor the spread of the generalist strategy (decrease
38 both θ_1^* and θ_2^*) are decreasing catastrophe probability, increasing fecundity
39 and increasing dispersal survival. Nurmi and Parvinen (2008) have also shown
40 that increasing the difference between the resource carrying capacities in the
41 patches (increasing the environmental heterogeneity) enlarges the parameter
42 domain where evolutionary branching of specialization may occur (by decreas-
43 ing θ_1^* and increasing θ_2^*). We now investigate how these results of Nurmi and
44 Parvinen (2008) change when dispersal propensity is not constant, but instead
45 evolves as a consequence of natural selection. This means that when calculating
46 the critical values of θ , we for each parameter combination assume that disper-

1 sal propensity has obtained the corresponding evolutionarily stable value. In
 2 Figure 15, we illustrate the way different ecological parameters affect the evo-
 3 lutionary properties of the generalist strategy in this case. In order to enable
 4 a simple comparison between the results, we follow exactly the presentation
 5 structure of Nurmi and Parvinen (2008). The upper row in Figure 15 illustrates
 6 the critical values of trade-off parameter θ as a function of various ecological
 7 parameters. The lower row illustrates the corresponding evolutionarily stable
 8 dispersal propensities. It is noteworthy that the scales of the vertical axes are
 9 different in each panel on the lower row. Thus only catastrophe probability
 10 and dispersal survival probability significantly affect the evolutionarily stable
 11 dispersal propensity.

12 The panels in the lower row of Figure 15 tempt one to conclude that the
 13 evolutionarily stable dispersal propensity of the generalist is always higher than
 14 the corresponding propensity of the specialist. Even though this conclusion is
 15 rather natural, it cannot be drawn from these results, since the value of the
 16 trade-off parameter is different for the black and grey curves.

17 The panels in the upper row of Figure 15 are qualitatively similar to those
 18 presented by Nurmi and Parvinen (2008) in regard to fecundity, environmental
 19 heterogeneity and dispersal survival. The panel illustrating the effect of a de-
 20 crease in the catastrophe probability is, however, qualitatively different. Nurmi
 21 and Parvinen (2008) suggested that decreasing the catastrophe probability fa-
 22vors the spread of the generalist strategy, but our results suggest that it enlarges
 23 the parameter domain where evolutionary branching of specialization may oc-
 24 cur. This difference is based on the fact that decreasing catastrophe probability
 25 also decreases the evolutionarily stable dispersal propensity and, consequently,
 26 further isolates the patches. Thus, even in the cases when branching is not
 27 possible within a single patch, it is possible at the metapopulation level, be-
 28 cause due to the increasing isolation each patch can finally be taken over by the
 29 specialist that is best adapted to the conditions in the patch type concerned.

30 When analyzing the evolutionary effects of environmental heterogeneity, one
 31 resource carrying capacity is kept constant while the other is increased. Besides
 32 increasing the environmental heterogeneity this also accelerates the local pop-
 33 ulation growth especially in small local populations. Thus, in the presentation
 34 structure adopted from Nurmi and Parvinen (2008), the evolutionary effects of
 35 environmental heterogeneity combine with the effects of fecundity. When we
 36 analyzed the environmental heterogeneity such that the sum of the carrying
 37 capacities was kept constant (the analysis is not illustrated), we observed that
 38 both the singular dispersal propensity and the critical value θ_1^* were virtually
 39 independent of the heterogeneity, whereas the critical value θ_2^* increased along
 40 with the environmental heterogeneity. Thus in Figure 15, the observation that
 41 increasing environmental heterogeneity enlarges the parameter domain in which
 42 the generalist strategy is evolutionarily attracting and increases dispersal is an
 43 artefact caused by accelerated local growth. However, the conclusion that in-
 44 creasing the environmental heterogeneity enlarges the parameter domain where
 45 evolutionary branching may occur, remains valid.

1 5. Discussion

2 5.1. Summary

3 We have studied the evolutionary change in a metapopulation context when
4 both dispersal propensity and specialization concerning resource usage can evolve
5 and are subject to natural selection. We observed that, for all viable paramete-
6 ter combinations, there is a unique singular dispersal propensity towards which
7 natural selection drives the dispersal propensity in a monomorphic population.
8 The numerical value of this singular propensity is mainly determined by the
9 probability to survive dispersal (π) and the catastrophe probability (c). The
10 type of this singular strategy (ESS or a branching point) is, on the other hand,
11 mainly determined by the dispersal survival (π), the amount of environmental
12 heterogeneity (differences between the resource carrying capacities), and, above
13 all, by the evolutionary attractor of the specialization strategy, i.e., whether
14 the metapopulation consists of specialists or generalists (determined mainly by
15 trade-off parameter θ).

16 In the presence of temporal variations (local catastrophes), dispersal affects
17 the evolution of specialization in a cumbersome, non-monotonous way (Ronce
18 and Kirkpatrick, 2001; Nurmi et al., 2008; Nurmi and Parvinen, 2008). In this
19 paper we have shown that allowing also dispersal propensity to evolve as a
20 consequence of natural selection greatly clarifies our conception of the evolu-
21 tion of specialization in spatially heterogenous models, because it allows us to
22 readily focus our analysis on the evolutionarily relevant dispersal propensities.
23 Especially the differences between our results and those of Nurmi and Parvinen
24 (2008) indicate that, when studying the evolution of specialization also evolution
25 of dispersal should be taken into account (see Figure 15).

26 The evolutionary simulations we have performed demonstrate that the evolu-
27 tion of dispersal is usually slower than the evolution of specialization, i.e.,
28 evolutionary forces influencing specialization are stronger than those influencing
29 dispersal. This phenomenon is rather natural, since the degree of specialization
30 always affects reproduction (see Equation (2)). Dispersal affects both the repro-
31 duction of the dispersers and the reproduction of those remaining. However, the
32 effect on the dispersers' fecundity depends crucially on how the original patch
33 and the target patch differ in terms of quality and crowdedness. Thus it requires
34 several generations and dispersal events to be able to observe the average effect
35 of dispersal on the dispersers' fecundity. On the other hand, the fecundity of
36 the remaining individuals is increased by dispersals only in crowded patches.

37 When two traits are evolving and there are significant differences in the
38 strength of the evolutionary forces influencing them, it is even possible that the
39 evolution of the faster evolving trait halts the evolution of the other. For exam-
40 ple, in Figures 3A, 4B-C, 6B, and 12B-C the evolution of specialization halts
41 the evolution of dispersal at the initial phase. This may occur, because when a
42 new mutant dispersal propensity comes up, it has initially a very small popu-
43 lation size that increases rather slowly even if the mutant is capable to invade
44 the population. New mutants usually come up before this mutant population
45 has reached a significant size. Consequently, since the mutations affect only one

1 trait at a time, the new mutants usually have a dispersal propensity inherited
2 from the initial resident population. If any of these mutants has a specializa-
3 tion strategy that is capable to invade the resident, this mutant (carrying the
4 original dispersal propensity) will increase rapidly in population size (due to the
5 stronger evolutionary forces) and outcompete the other strategies, including the
6 one in which the new dispersal propensity results in higher fitness compared to
7 the initial resident population. This phenomenon is based on clonal interfer-
8 ence. It is possible in our model since there is no pleiotropy or recombination
9 (Gerrish and Lenski, 1998).

10 However, the core of our results is associated with the trimorphic coexistence
11 of generalists and specialists. Such coexistence was first demonstrated in a model
12 compiled by Wilson and Yoshimura (1994). In their model, the coexistence was
13 found not to be evolutionarily attainable in an initially monomorphic popu-
14 lation. In other words, the evolution of an initially monomorphic population
15 never leads to the trimorphic coexistence if mutations are assumed small and
16 infrequent (Egas et al., 2004). Later on, trimorphic coexistence has been shown
17 evolutionarily attainable under cyclic resource dynamics (Abrams, 2006a,b) or
18 when the assumptions concerning the consumer behavior are relatively restric-
19 tive (Egas et al., 2004). Nurmi and Parvinen (2008) have shown that, even
20 though the possibility of trimorphic coexistence is typical to our modeling ap-
21 proach, it is never evolutionarily attainable when only specialization can evolve.
22 Our results show that when also dispersal can evolve and several patch types
23 exist, coexistence becomes evolutionarily attainable even under equilibrium dy-
24 namics and in a model that is not customized for this purpose.

25 In our model, a typical evolutionary path leading to trimorphic coexistence
26 starts with evolutionary branching of dispersal in a metapopulation consist-
27 ing of generalist individuals (or in more general, in a metapopulation where
28 individuals are not fully specialized). In the consequent competition, the less
29 dispersive morph may benefit from specialism, which finally leads to a trimor-
30 phic metapopulation comprising one abundantly dispersing generalist and two
31 scarcely dispersing specialists. This scenario is rare in environments with only
32 two patch types but more common when there are at least three patch types.

33 In our model, on the other hand, the local dynamics are determined by
34 the Beverton–Holt equation featuring only monotonous convergence to fixed
35 points. Cyclic or chaotic local population dynamics may promote evolutionary
36 branching of dispersal in a metapopulation model (see e.g. Parvinen (2006) and
37 the references therein). Thus it is an interesting task for the future to study the
38 joint evolution of specialization and dispersal under non-equilibrium dynamics.

39 In general, comparisons between studies focusing on the joint evolution of
40 specialization and dispersal are rather cumbersome. There are only few studies
41 of this kind and they all focus on different questions from different viewpoints
42 (Kisdi, 2002; Hanski and Heino, 2003; Heinz et al., 2009).

43 Kisdi (2002) has studied a model of two patches, in which there appears
44 adaptation to the different local conditions. Compared to our model, she as-
45 sumed the temporal variations to be rather mild: "good" and "bad" years that
46 occur randomly and independently in each patch. These temporal variations

1 were not influential enough to allow selection for dispersal. Thus, a high degree
2 of dispersal or generalism usually appeared only as a response to the competi-
3 tion with low-dispersal specialists. This contrasts with our model, in which the
4 singular dispersal propensity may take on any value depending on the dispersal
5 survival and the catastrophe probability. Moreover, sufficient changes in trade-
6 off parameter θ always determine the endpoint of the evolution of specialization
7 independent of the other parameter values.

8 Heinz et al. (2009) have studied the joint evolution of dispersal distance and
9 local adaptation in an environment with a continuously varying character by
10 means of individual based simulation models. Their viewpoint is very different
11 from ours and this prevents direct comparisons between results. However in
12 their model, predictions based on asexual model are, qualitatively speaking,
13 principally consistent with the predictions derived from the sexual model.

14 Hanski and Heino (2003) have carried out a simulation-based case study
15 on the evolution of dispersal and host-plant preference (specialization) among
16 Glanville fritillary butterflies *Melitaea cinxia*. In the model parametrized on
17 the basis of observing the actual metapopulation in the Åland Islands in south
18 western Finland, the dispersal propensity always evolved to rather low value
19 (≈ 0.1). Dispersal dimorphism was not observed, and specialization in a specific
20 host plant did not significantly affect the evolution of dispersal. The females
21 were predicted to prefer the more abundant host plant in each patch. This
22 preference, on the other hand, was strongly affected by the distribution of the
23 host plants in the surrounding patch network. However, absolute specialism
24 involving the exclusion of the other host plant was never observed. It is an
25 interesting task for the future to find out whether our model can be fine-tuned
26 to cover the dynamics of *Melitaea* and used to predict the evolving ecological
27 and evolutionary dynamics.

28 5.2. Main features and limitations of the modeling approach

29 The metapopulation theory concerning the evolution of specialization was
30 initiated by Parvinen and Egas (2004), who integrated the context of structured
31 metapopulations to the long tradition of habitat specialization models (Levins,
32 1962; van Tienderen, 1991; Brown and Pavlovic, 1992; Kisdi, 2002). Tradition-
33 ally, habitat specialization models have not rationalized the differences between
34 various patches. Nurmi et al. (2008) underpinned these differences by con-
35 sidering the distribution of resources. According to them, each patch type is
36 characterized by the availability of two resources. Nurmi et al. (2008) studied
37 specialization concerning the utilization of resources. Their model is a straight-
38 forward generalization of the habitat specialization models in a sense that, it is
39 capable to assume any finite number of patch types, but in the case with two
40 patch types it is equivalent to the habitat specialization models.

41 Once the explicit resource distribution was included in the model, there
42 arose a need for modeling their dynamics as well. Therefore, Nurmi and Parvi-
43 nen (2008) underpinned the metapopulation dynamics with a continuous-time
44 resource–consumer dynamics adopted from Geritz and Kisdi (2004), and com-
45 menced to study the evolution of specialization concerning resource utilization.

1 The model used in this paper was the same as the one analyzed by Nurmi
2 and Parvinen (2008), except that here we assumed also dispersal to evolve as
3 consequence of natural selection.

4 A spatial structure, either explicit or implicit, is a necessity for any model
5 that involves dispersal. Mere spatial variation is not, however, a sufficient con-
6 dition for evolution to favor dispersal. Instead, spatial heterogeneity usually
7 hinders dispersal, especially if the population is capable to adapt to local con-
8 ditions. This is because the population size is at its largest value in the patches
9 to which the species is best adapted and, in consequence, the dispersers risk mi-
10 grating to a less favorable habitat (Gadgil, 1971; Hastings, 1983; Parvinen, 1999;
11 Gyllenberg et al., 2002). Previous studies have shown that, in addition to local
12 adaptation and spatial variation, the main factors influencing the evolution of
13 dispersal include temporal variations, kin selection, inbreeding avoidance, direct
14 costs of dispersal, and interspecific interactions (see e.g. Clobert et al. (2001)
15 and the related references).

16 The temporal variations in our model occur rather drastically in the form of
17 catastrophes eradicating entire local populations. More subtle manifestations of
18 variation would probably incline the evolution towards a lower dispersal propen-
19 sity. Our results agree with the general conception according to which increasing
20 the frequency of environmental disturbances (catastrophes) increases dispersal
21 provided that the ecological parameters are not close to the viability boundaries.
22 Also spatial heterogeneity and direct costs of dispersal are integral parts of all
23 structured metapopulation models. Our results contribute to the general knowl-
24 edge by pointing out that the costs of dispersal combined with local adaptation
25 substantially determine whether dispersal branching is possible.

26 Even though we explicitly model the population dynamics in each patch,
27 our model is not adequate for the analysis kin selection. In a model with finite
28 local populations, each dispersing individual benefits those relatives that do not
29 disperse by reducing crowding in the patch. However, we assume that the local
30 populations are large (i.e., the local population dynamics are described deter-
31 ministically). Thus in the initial phase of an invasion, the effect of a mutant
32 population on the population dynamics is ignorable even locally. Thus a dis-
33 persing mutant is not able to benefit those relatives that do not disperse. Also
34 inbreeding depression is, unfortunately, beyond the scope of this model since
35 the related evolutionary analysis is based on the adaptive dynamics approach
36 that assumes a rather simple genetic architecture and clonal reproduction.

37 Enabling the analysis of inbreeding depression is not the only reason that
38 encourages one to, in the future, extend this model to cover sexual reproduction
39 and more complicated genetic architectures. There are several studies suggest-
40 ing that the phenotypic models of evolution, to some extent, enable one to
41 predict the course of evolution also in sexually reproducing populations (May-
42 nard Smith, 1981; Weissing, 1996; Taylor, 1996; Heinz et al., 2009). The major-
43 ity of these studies, however, focuses on models lacking a spatial structure. In
44 metapopulation models, the situation is complicated by the fact that a globally
45 rare mutant may simultaneously be locally prevailing in some patches. There-
46 fore the possible existence of mutant homozygotes should not be ignored in the

1 invasion analysis, either (Ravigné et al., 2006; Parvinen and Metz, 2008). On
2 the other hand, a spatially heterogenous population structure may assist the
3 appearance of assortative mating, which together with disruptive selection may
4 enable sympatric speciation (Dieckmann and Doebeli, 1999; Geritz and Kisdi,
5 2000).

6 Whereas the evolution of dispersal always takes place in the balance be-
7 tween the costs and benefits of dispersal, the trade-off between the abilities
8 of an individual to consume different resources needs to be explicitly modeled
9 (Joshi and Thompson, 1995; Fry, 1996). The ecological discrete-time dynam-
10 ics in our model have mechanistic underpinnings in continuous-time resource-
11 consumer dynamics except for trade-off parameter θ determining the shape (con-
12 vexity/concavity) of the trade-off function that crucially affects the evolution-
13 ary dynamics of specialization. Unfortunately, mechanistic determination of the
14 trade-off function is possible only in a specific ecological setting, not generally.
15 In our model, only the case featuring a linear trade-off ($\theta = 0$) offers a mech-
16 anistic biological interpretation. According to it, trade-offs arise purely from a
17 search-time allocation between the two resources. In this case the evolution of
18 specialization in a monomorphic population always leads to generalism forming
19 either an evolutionary endpoint or a branching point. Our modeling approach
20 favors generalists as dispersal occurs randomly, i.e., dispersers are not able to
21 choose their target patches. Including different manifestations of habitat selec-
22 tion might benefit specialists and enable evolution leading to a monomorphic
23 specialist population even in the case of a linear trade-off (Ravigné et al., 2009).

24 Even though we studied the joint evolution of two different traits, we did
25 not explicitly consider the genetic linkage or epistasis, because the genetic ar-
26 chitecture we assumed was too simple for a rational study of these subjects.
27 Since we assumed that the inheritance was clonal and that mutations only af-
28 fected only one trait at a time, we indeed assumed a complete genetic linkage
29 between the two traits. On the other hand, since we assumed that the two
30 traits could evolve independently and that all different trait combinations were
31 possible, pleiotropy could not affect the evolutionary dynamics. The adaptive
32 dynamics approach also provides tools for the analysis of the case where both
33 traits could evolve simultaneously. Leimar (2001, 2009) has shown that in this
34 case, different mutational variance-covariance structures and fitness interactions
35 may crucially affect the evolutionary dynamics. Furthermore, Ravigné et al.
36 (2009) have shown that the joint evolution of habitat specialization and habi-
37 tat selection may crucially affect the specialization process. In their model the
38 possibility of pleiotropic mutations promoted evolutionary branching of special-
39 ization. Pleiotropy presumably has a resembling effect also in our model. This
40 effect, however, is likely milder since habitat selection is expected to have much
41 stronger effect on specialization than randomly targeted dispersal. Pleiotropy
42 might, as well, promote the evolution to the trimorphic coexistence of specialists
43 and a generalist. Unfortunately, when mutations do not occur independently
44 or do not affect only one trait at a time, it is difficult find any general results
45 concerning the evolutionary dynamics and, above all, it is no longer possible to
46 fully illustrate different evolutionary scenarios by plotting the fitness gradient

1 isoclines. Especially, pleiotropy may affect the invadability of a singular strat-
 2 egy: a singular strategy that is uninvadable by mutants with either different
 3 dispersal propensity or different specialization strategy may be invadable by a
 4 mutant different both in dispersal and specialization (Leimar, 2001). On the
 5 other hand, even the case without pleiotropy involves the main features of the
 6 joint evolution we wish to present here. Therefore, we postpone dealing with
 7 pleiotropic mutations to our future research.

8 **A. Simulation procedure**

9 We run evolutionary simulations in an environment consisting of 1000 patches.
 10 The procedure is as follows:

- 11 1. Iterate the metapopulation dynamics for 1000 generations.
- 12 2. Remove all the strategies the metapopulation size of which has decreased
 13 below 25 percent of the size initial size at the time the mutant entered the
 14 metapopulation. These strategies are considered extinct.
- 15 3. If the number of strategies in the metapopulation is larger than 25, go
 16 back to step 1. In order to speed up the simulation we limit the number
 17 of coexisting strategies to 25.
- 18 4. Pick one strategy that will mutate. The probability to pick a certain
 19 strategy is determined by the strategy's metapopulation size divided by
 20 the total metapopulation size.
- 21 5. Toss a coin to decide, whether the mutation will affect dispersal propensity
 22 or specialization.
- 23 6. Pick the size of the mutation using normal distribution, the expectation
 24 being zero and the standard deviation 0.012. It is plausible to use the
 25 same distribution for both traits since they receive values from the same
 26 interval $[0, 1]$.
- 27 7. Check that the new strategy belongs to the strategy space and differs
 28 sufficiently from the present strategies, i.e., the Euclidian distance between
 29 the strategies in the (e, s) -plane is at least 0.006. If not, continue from
 30 step 4.
- 31 8. Continue from step 1.

32 **References**

- 33 Abrams, P., 2006a. Adaptive Change in the Resource-Exploitation Traits of
 34 a Generalist Consumer: The Evolution and Coexistence of Generalist and
 35 Specialists. *Evolution* 60, (427–439).
- 36 Abrams, P., 2006b. The Prerequisites for and Likelihood of Generalist-Specialist
 37 Coexistence. *Am. Nat.* 167, (329–342).
- 38 Boggs, C. L., Day, B., 2004. Resource Specialization in Puddling Lepidoptera.
 39 *Environ. Entomol.* 33, (1020–1024).

- 1 Brown, J., Pavlovic, N., 1992. Evolution in Heterogeneous Environments: Ef-
2 fects of Migration on Habitat Specialization. *Evol. Ecol.* 6, (360–382).
- 3 Clobert, J., Danchin, E., Dhondt, A. A., Nichols, J. D., 2001. *Dispersal*. Oxford
4 University Press.
- 5 Dennis, R. L. H., Shreeve, T. K., Van Dyck, H., 2006. Habitats and resources:
6 the need for a resource-based definition to conserve butterflies. *Biodiv. Con-*
7 *serv.* 15, (1943–1966).
- 8 Dieckmann, U., Doebeli, M., 1999. On the origin of species by sympatric speci-
9 ation. *Nature* 400, 354–357.
- 10 Dieckmann, U., Law, R., 1996. The Dynamical Theory of Coevolution: A
11 Derivation from Stochastic Ecological Processes. *J. Math. Biol.* 34, (579–612).
- 12 Doebeli, M., Ruxton, G. D., 1997. Evolution of dispersal rates in metapopulation
13 models: branching and cyclic dynamics in phenotype space. *Evolution* 51,
14 (1730–1741).
- 15 Durinx, M., Metz, J., Meszéna, G., 2008. Adaptive dynamics for physiologically
16 structured population models. *J. Math. Biol.* 56, (673–742).
- 17 Egas, M., Dieckmann, U., Sabelis, M., 2004. Evolution restricts the Coexistence
18 of Specialists and Generalists: The Role of the Trade-off Structure. *Am. Nat.*
19 163, (518–531).
- 20 Fry, J. D., 1996. The evolution of host specialization: Are trade-offs overrated?
21 *Am. Nat.* 148, (S84–S107).
- 22 Futuyma, D., Moreno, G., 1988. The evolution of ecological specialization.
23 *Annu. Rev. Ecol. Syst.* 19, (207–233).
- 24 Gadgil, M., 1971. Dispersal: Population Consequences and Evolution. *Ecology*
25 52, (253–261).
- 26 Geritz, S. A. H., Kisdi, É., 2000. Adaptive Dynamics in Diploid, Sexual Pop-
27 ulations and the Evolution of Reproductive Isolation. *Proc. R. Soc. Lond. B*
28 267, (1671–1678).
- 29 Geritz, S. A. H., Kisdi, É., 2004. On the mechanistic underpinning of discrete-
30 time population models with complex dynamics. *J. Theor. Biol.* 228, (261–
31 269).
- 32 Geritz, S. A. H., Kisdi, É., Meszéna, G., Metz, J. A. J., 1998. Evolutionary Sin-
33 gular Strategies and the Adaptive Growth and Branching of the Evolutionary
34 Tree. *Evol. Ecol.* 12, (35–57).
- 35 Gerrish, P. J., Lenski, R. E., 1998. The fate of competing beneficial mutations
36 in an asexual population. *Genetica* 102-103, (127–144).

- 1 Gyllenberg, M., Metz, J. A. J., 2001. On Fitness in Structured Metapopulations.
2 J. Math. Biol. 43, (545–560).
- 3 Gyllenberg, M., Parvinen, K., Dieckmann, U., 2002. Evolutionary Suicide and
4 Evolution of Dispersal in Structured Metapopulations. J. Math. Biol. 45, (79–
5 105).
- 6 Hanski, I., Heino, M., 2003. Metapopulation-level Adaption of Insect Host Plant
7 Preference and Extinction-Colonization Dynamics in Heterogeneous Land-
8 scapes. Theor. Pop. Biol. 64, (281–290).
- 9 Hanski, I., Singer, M. C., 2001. Extinction-Colonization Dynamics and Host-
10 Plant Choice in Butterfly Metapopulations. Am. Nat. 158, (341–353).
- 11 Harrison, S., Thomas, C. D., 1992. Spatial Dynamics of a Patchily Distributed
12 Butterfly Species. J. Anim. Ecol. 61, (437–446).
- 13 Hastings, A., 1983. Can Spatial Variation Alone Lead to Selection for Dispersal?
14 Theor. Popul. Biol. 24, (244–251).
- 15 Heinz, Simone, K., Mazzucco, R., Dieckmann, U., 2009. Speciation and the
16 evolution of dispersal along environmental gradients. Evol. Ecol. 23, (53–70).
- 17 Holt, R. D., McPeck, M., 1996. Chaotic population dynamics favors the evolu-
18 tion of dispersal. Am. Nat. 148, (709–718).
- 19 Johnson, M. L., Gaines, M. S., 1990. Evolution of Dispersal: Theoretical Models
20 and Empirical Tests Using Birds and Mammals. Annu. Rev. Ecol. Syst. 21,
21 (449–480).
- 22 Joshi, A., Thompson, J. N., 1995. Trade-offs and the evolution of host special-
23 ization. Evol. Ecol. 9, (82–92).
- 24 Kisdi, É., 2002. Dispersal: Risk Spreading versus Local Adaptation. Am. Nat.
25 159, (579–596).
- 26 Leimar, O., 2001. Evolutionary Change and Darwinian Demons. Selection 1-2,
27 (65–72).
- 28 Leimar, O., 2009. Multidimensional convergence stability. Evol. Ecol. Res. 11,
29 (191–208).
- 30 Levin, S. A., Muller-Landau, H. C., Nathan, R., Chave, J., 2003. The Ecology
31 and Evolution of Seed Dispersal: A Theoretical Perspective. Annu. Rev. Ecol.
32 Evol. Syst. 34, (575–604).
- 33 Levins, R., 1962. Theory of Fitness in a Heterogeneous Environment. I. The
34 Fitness Set and Adaptive Function. Am. Nat. 96, (361–373).
- 35 Mathias, A., Kisdi, É., Olivieri, I., 2001. Divergent Evolution of Dispersal in a
36 Heterogeneous Landscape. Evolution 55, (246–259).

- 1 Maynard Smith, J., 1981. Will a sexual population evolve to an ESS. *Am. Nat.*
2 117, (1015–1018).
- 3 McPeck, M. A., Holt, R. D., 1992. The Evolution of Dispersal in Spatially and
4 Temporally Varying Environments. *Am. Nat.* 140, (1010–1027).
- 5 Metz, J. A. J., Gyllenberg, M., 2001. How Should We Define Fitness in Struc-
6 tured Metapopulation Models? Including an Application to the Calculation of
7 Evolutionarily Stable Dispersal Strategies. *Proc. R. Soc. Lond. B* 268, (499–
8 508).
- 9 Metz, J. A. J., Nisbet, R., Geritz, S. A. H., 1992. How Should We Define Fitness
10 for General Ecological Scenarios? *Trends Ecol. Evol.* 7, (198–202).
- 11 Nurmi, T., Geritz, S. A. H., Parvinen, K., Gyllenberg, M., 2008. Evolution
12 of Specialization on Resource Utilization in Structured Metapopulations. *J.*
13 *Biol. Dyn.* 2, (297–322).
- 14 Nurmi, T., Parvinen, K., 2008. On the evolution of specialization with a mech-
15 anistic underpinning in metapopulations. *Theor. Pop. Biol.* 73, (222–243).
- 16 Parvinen, K., 1999. Evolution of migration in a metapopulation. *Bull. Math.*
17 *Biol.* 61, (531–550).
- 18 Parvinen, K., 2002. Evolutionary Branching of Dispersal Strategies in Struc-
19 tured Metapopulations. *J. Math. Biol.* 45, (106–124).
- 20 Parvinen, K., 2006. Evolution of dispersal in a structured metapopulation model
21 in discrete time. *Bull. Math. Biol.* 68, (655–678).
- 22 Parvinen, K., Dieckmann, U., Gyllenberg, M., Metz, J., 2003. Evolution of
23 dispersal in metapopulations with local density dependence and demographic
24 stochasticity . *J. Evol. Biol.* 16, (143–153).
- 25 Parvinen, K., Egas, M., 2004. Dispersal and the Evolution of Specialisation in
26 a two-habitat type metapopulation. *Theor. Popul. Biol.* 66, (233–248).
- 27 Parvinen, K., Metz, J. A., 2008. A novel fitness proxy in structured locally
28 finite metapopulations with diploid genetics, with an application to dispersal
29 evolution. *Theor. Popul. Biol.* 73, (517–528).
- 30 Ravigné, V., Dieckmann, U., Olivieri, I., 2009. Live Where You Thrive: Joint
31 Evolution of Habitat Choice and Local Adaptation Facilitates Specialization
32 and Promotes Diversity . *Am. Nat.* 174, (E141–E169).
- 33 Ravigné, V., Olivieri, I., Gonzalez-Martinez, S. C., Rousset, F., 2006. Selec-
34 tive interactions between short-distance pollen and seed dispersal in self-
35 compatible species. *Evolution* 60, (2257–2271).
- 36 Ronce, O., 2007. How Does It Feel to Be Like a Rolling Stone? Ten Questions
37 About Dispersal Evolution. *Annu. Rev. Ecol. Syst.* 38, (231–253).

- 1 Ronce, O., Kirkpatrick, M., 2001. When sources become sinks: Migrational
2 meltdown in heterogeneous habitats. *Evolution* 55, (1520–1531).
- 3 Ronce, O., Perret, F., Olivieri, I., 2000. Evolutionarily stable dispersal rates do
4 not always increase with local extinction rates. *Am. Nat.* 155, 485–496.
- 5 Rueffler, C., Egas, M., Metz, J., 2006. Evolutionary Predictions Should Be
6 Based on Individual-Level Traits. *Am. Nat.* 168, (E148–E162).
- 7 Smedley, S. R., Eisner, T., 1995. Sodium Uptake by Puddling in a Moth. *Science*
8 270, (1816–1818).
- 9 Taylor, P., 1996. The Selection Differential in Quantitative Genetics and ESS
10 Models. *Evolution* 5, (2106–2110).
- 11 van Tienderen, P., 1991. Evolution of Generalists and Specialists in Spatially
12 Heterogenous Environments. *Evolution* 45, (1317–1331).
- 13 Watkinson, A. R., Sutherland, W. J., 1995. Sources, sinks and pseudo-sinks. *J.*
14 *Anim. Ecol.* 64, (126–130).
- 15 Weissing, F., 1996. Genetic versus phenotypic models of selection: can genetics
16 be neglected in a long-term perspective. *J. Math. Biol.* 34, (533–555).
- 17 Wilson, D. S., Yoshimura, J., 1994. On the Coexistence of Specialists and Gen-
18 eralists. *Am. Nat.* 144, (692–707).

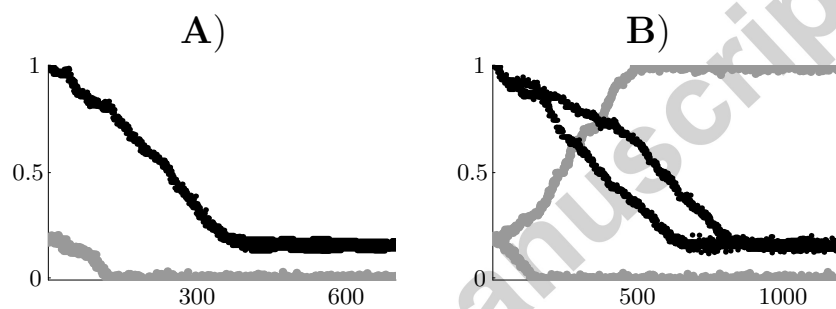


Figure 5: Two evolutionary simulations with identical ecological and evolutionary parameters and the same initial state ($e = 1, s = 0.19$). The simulations have different evolutionary endpoints because of random mutations. The parameter values identical with the ones in Figure 1C.

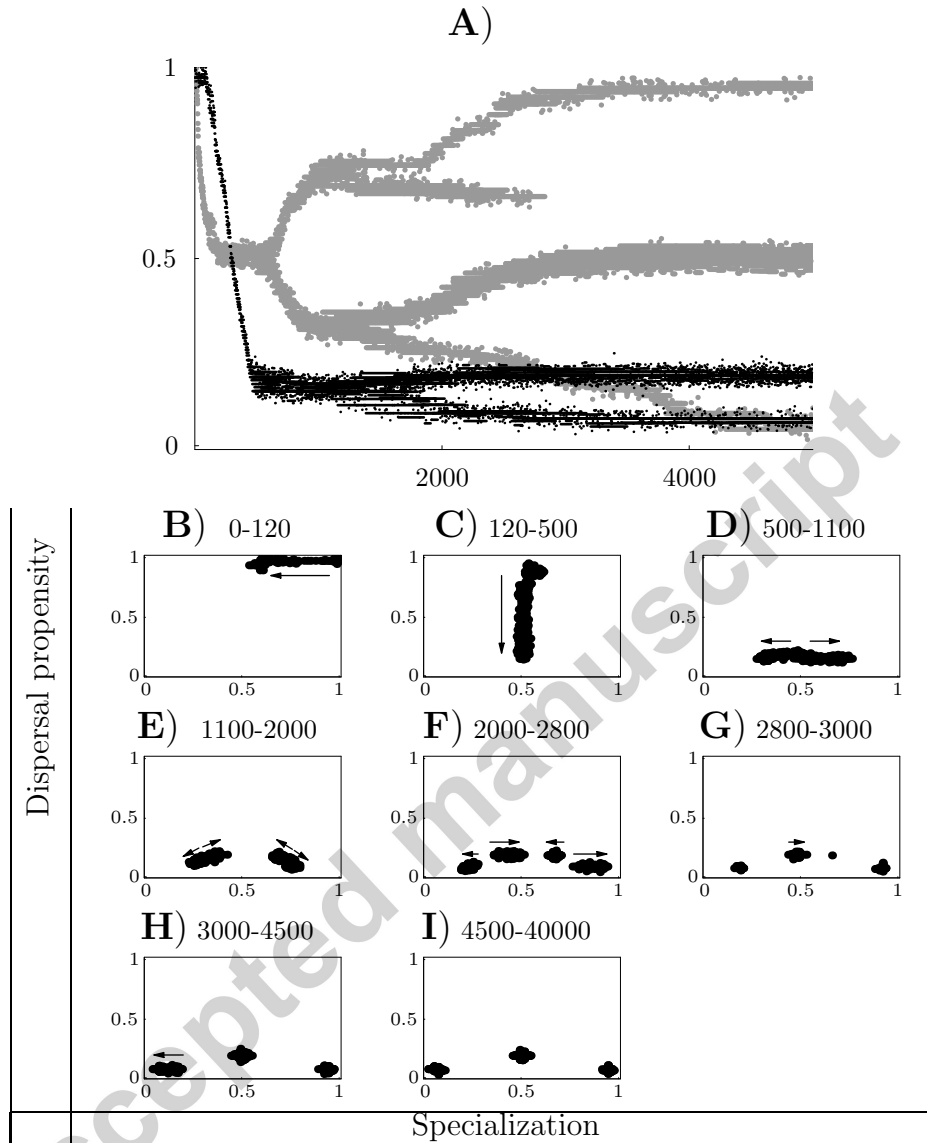


Figure 6: Panel A illustrates the strategies present in the metapopulation as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e . Each dot in Panels B-I represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s . The arrows in Panels B-I indicate the direction of evolution. The initial strategy $(e, s) = (1, 1)$. The simulation ended in a trimorphic population using strategies $(e, s) \approx (0.2, 0.5)$, $(0.1, 0.1)$ and $(0.1, 0.9)$. The other parameter values correspond to the ones in Figure 1G.

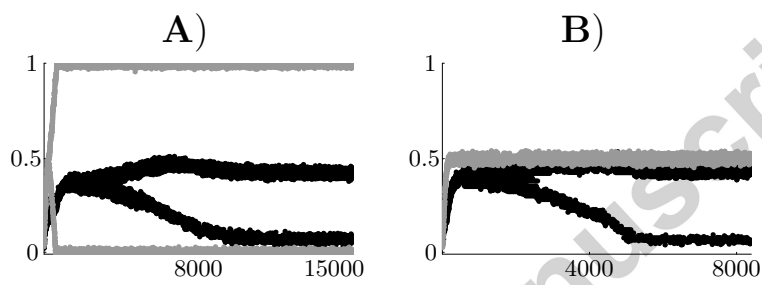


Figure 7: Locally symmetric environments: Strategies present in the metapopulation during an evolutionary simulation. Grey curves = the specialization component s of the strategy, black curves = the dispersal component e . The parameter values are the same as in the corresponding panels in Figure 2. Initial strategy $(e, s) = (0.05, 0.05)$.

Panel A: The simulation ends up in a quadrimorphic population using strategies $(e, s) \approx (0.44, 0)$, $(0.44, 1)$, $(0.07, 0)$ and $(0.07, 1)$.

Panel B: The simulation ends up in a dimorphic population using strategies $(e, s) \approx (0.07, 0.5)$ and $(0.44, 0.5)$.

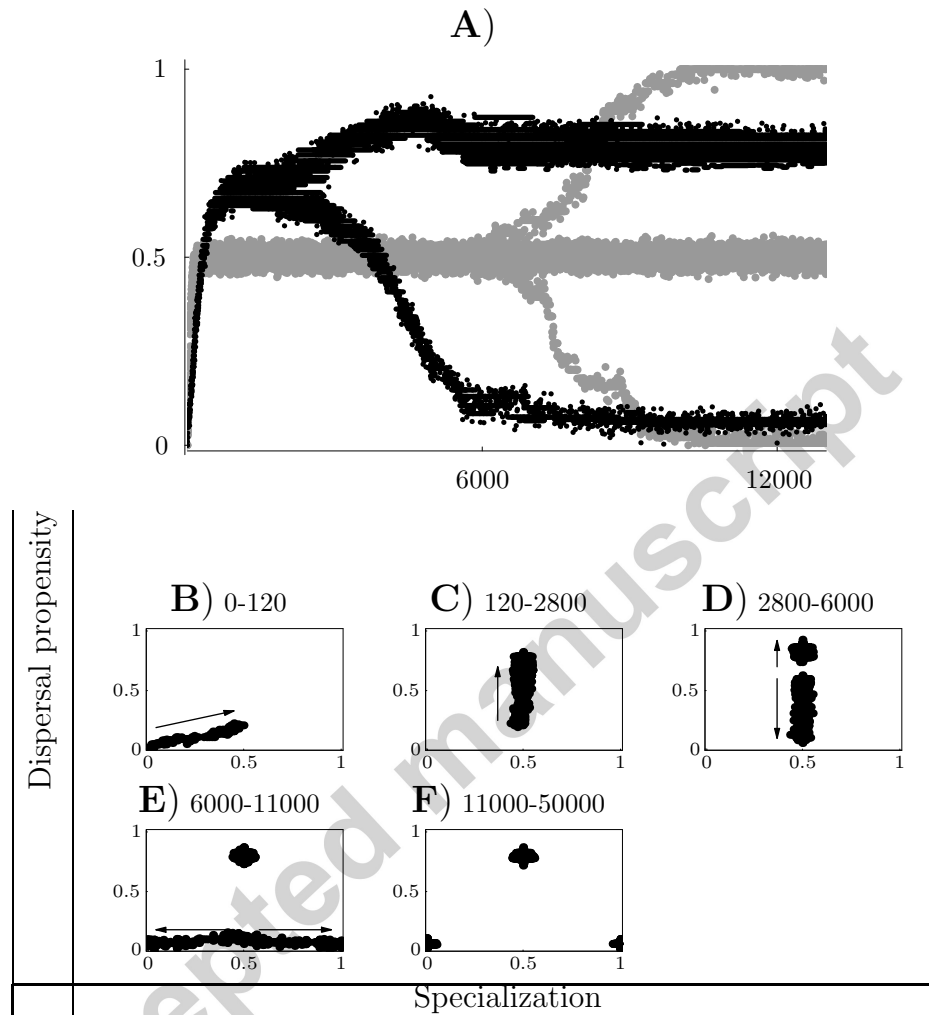
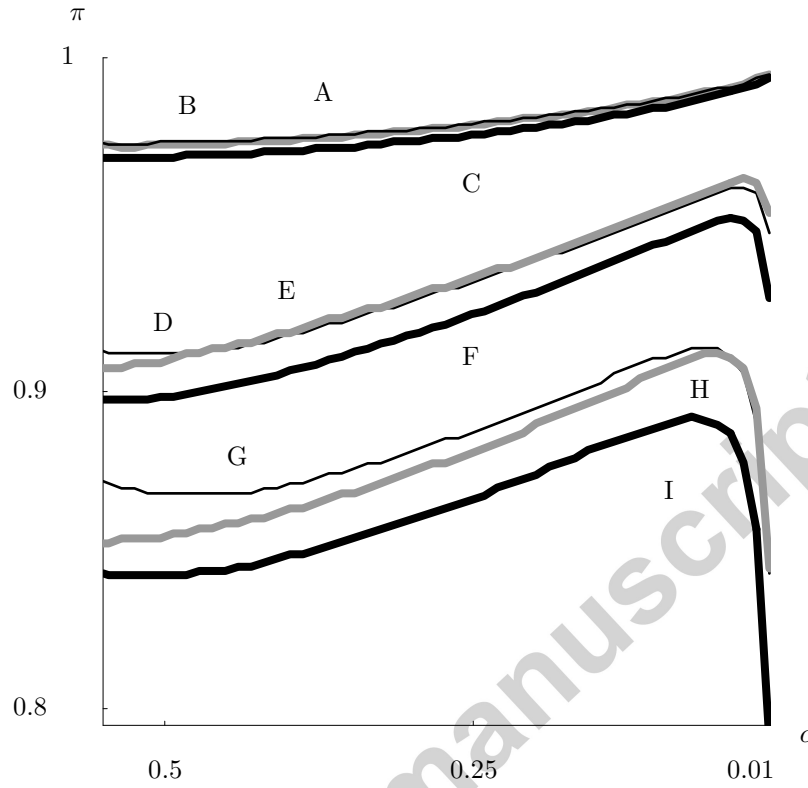


Figure 8: Panel A illustrates the strategies present in the metapopulation as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e . Each dot in Panels B-F represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s . The arrows in Panels B-F indicate the direction of evolution. The initial strategy $(e, s) = (0.1, 0.1)$. The simulation ended in a trimorphic metapopulation using strategies $(e, s) \approx (0.1, 0)$, $(0.1, 1)$ and $(0.8, 0.5)$. The other parameter values correspond to the ones in Figure 2C.



Curve	Color	Patch type 1			Patch type 2			Patch type 3			K^*
		p_1	K_1^1	K_2^1	p_2	K_1^2	K_2^2	p_3	K_1^3	K_2^3	
A	Thin black	0.125	3	1	0.125	1	3	0.75	2	2	2
B	Grey	0.375	3	1	0.375	1	3	0.25	2	2	2
C	Thick black	0.25	3	1	0.25	1	3	0.5	2	2	2
D	Thin black	0.125	5	1	0.125	1	5	0.75	1	1	1.5
E	Grey	0.375	5	1	0.375	1	5	0.25	1	1	2.5
F	Thick black	0.25	5	1	0.25	1	5	0.5	1	1	2
G	Thin black	0.125	8	2	0.125	2	8	0.75	1	1	2
H	Grey	0.375	8	2	0.375	2	8	0.25	1	1	4
I	Thick black	0.25	8	2	0.25	2	8	0.5	1	1	3

Figure 9: Type of the singular dispersal propensity (ESS or a branching point) as a function of catastrophe probability c and dispersal survival π in a metapopulation consisting of unbiased generalists. Different curves correspond to different resource distributions. Above the curves the singular dispersal propensity is a branching point and below an ESS. Curves drawn with same style correspond to cases with same fraction of patches acting as sources in the metapopulation dynamics. Column K^* = the average resource carrying capacity in the corresponding patch type (same for both resource in symmetric environments). The other parameter values are $\theta = 0.1$ and $\lambda = 3$.

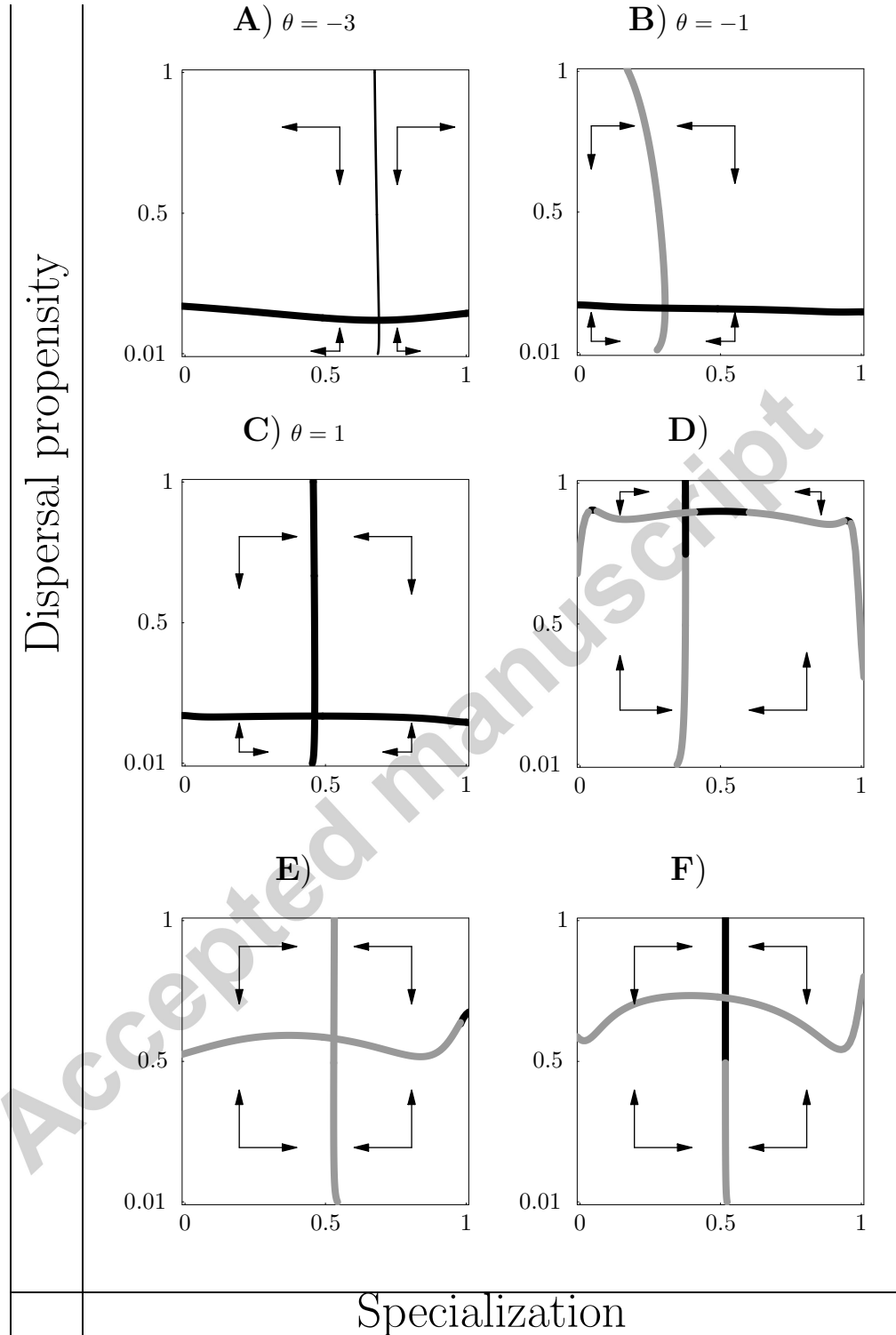


Figure 10: **Asymmetric environments comprising two patch types:** Evolutionarily singular specialization strategies as a function of dispersal propensity (horizontal axis) and singular dispersal propensity as a function of specialization (vertical axis). Thick black curve = CSS, thick grey curve = branching point, thin black curve = evolutionary repeller. (A-D): swapped carrying capacities in patches types with asymmetric proportions. Other parameter values in Panels A, B and C: $c = 0.05$, $\pi = 0.8$, $\lambda = 3$, $K_1^1 = K_2^2 = 3$, $K_1^2 = K_2^1 = 1$ and $p_1 = 0.1$, $p_2 = 0.9$, Panel D: $c = 0.1$, $\pi = 0.99$, $\theta = 0.1$, $\lambda = 1.5$, $K_1^1 = K_2^2 = 10$, $K_1^2 = K_2^1 = 1$, $p_1 = 0.2$, and $p_2 = 0.8$. (E-F) non-swapped carrying capacities in patch types with equal proportions ($p_1 = p_2 = 0.5$). Panel E: $\pi = 0.98$, $\theta = -1$, $K_1^1 = 2$, and $K_2^2 = 3$. Panel F: $\pi = 0.99$, $\theta = 0.01$, $K_1^1 = 3$, and $K_2^2 = 4$. Common parameter values in panels E and F: $c = 0.05$, $\lambda = 3$, $K_1^1 = 2$, $K_2^1 = 1$.

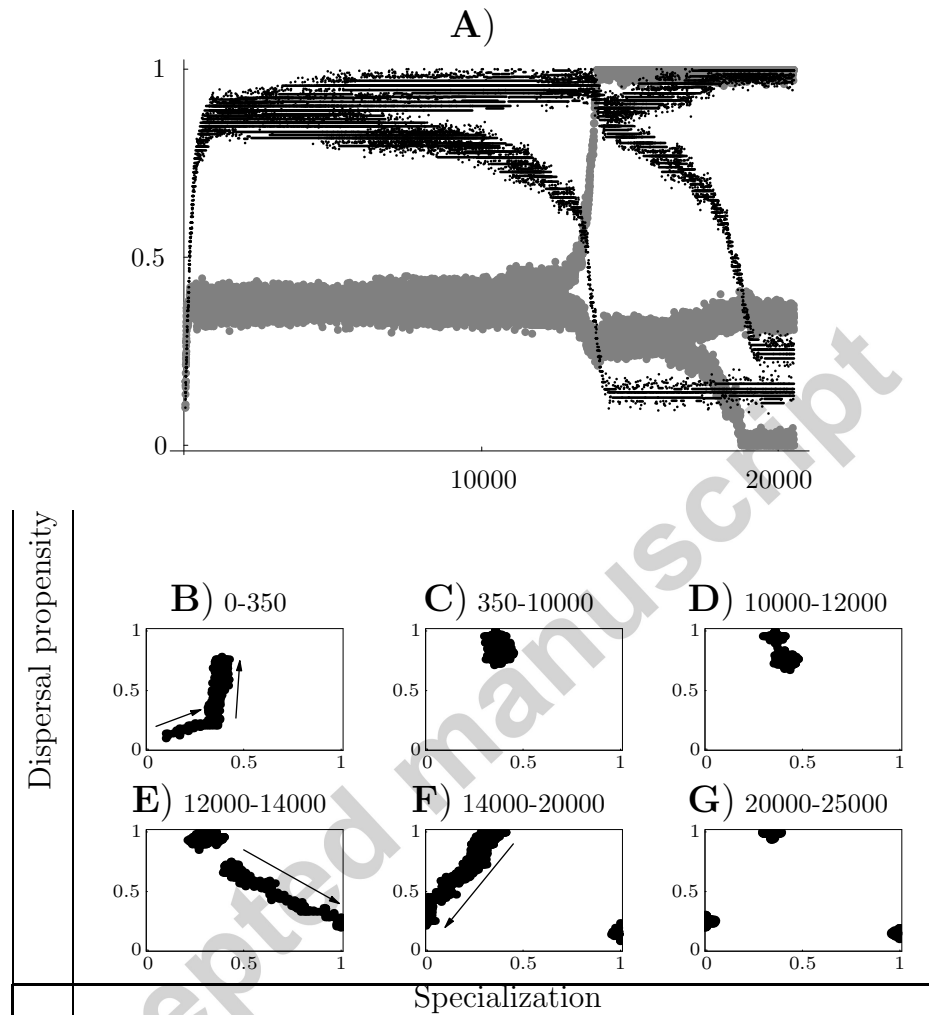


Figure 11: Panel A illustrates the strategies present in the metapopulation as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e . Each dot in Panels B-G represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s . The arrows in Panels B-G indicate the direction of evolution. The initial strategy $(e, s) = (0.1, 0.1)$. The simulation ended in a trimorphic population using strategies $(e, s) \approx (0.25, 0)$, $(1, 0.4)$ and $(0.1, 1)$. The other parameter values correspond to the ones in Figure 10D.

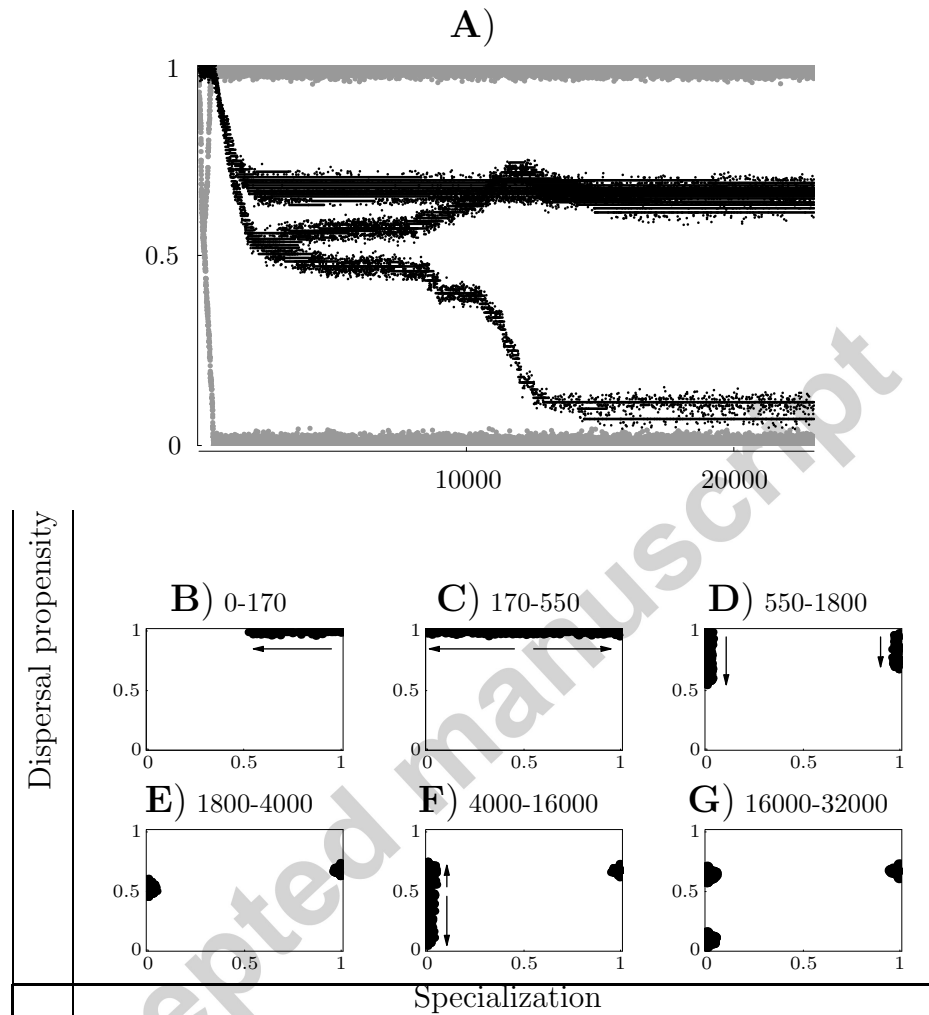


Figure 12: Panel A illustrates the strategies present in the metapopulation as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e . Each dot in Panels B-G represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s . The arrows in Panels B-G indicate the direction of evolution. The initial strategy $(e, s) = (1, 1)$. The simulation ended in a trimorphic population using strategies $(e, s) \approx (0.1, 0)$, $(0.65, 0)$ and $(0.67, 1)$. Parameter values correspond to the ones in Figure 10E.

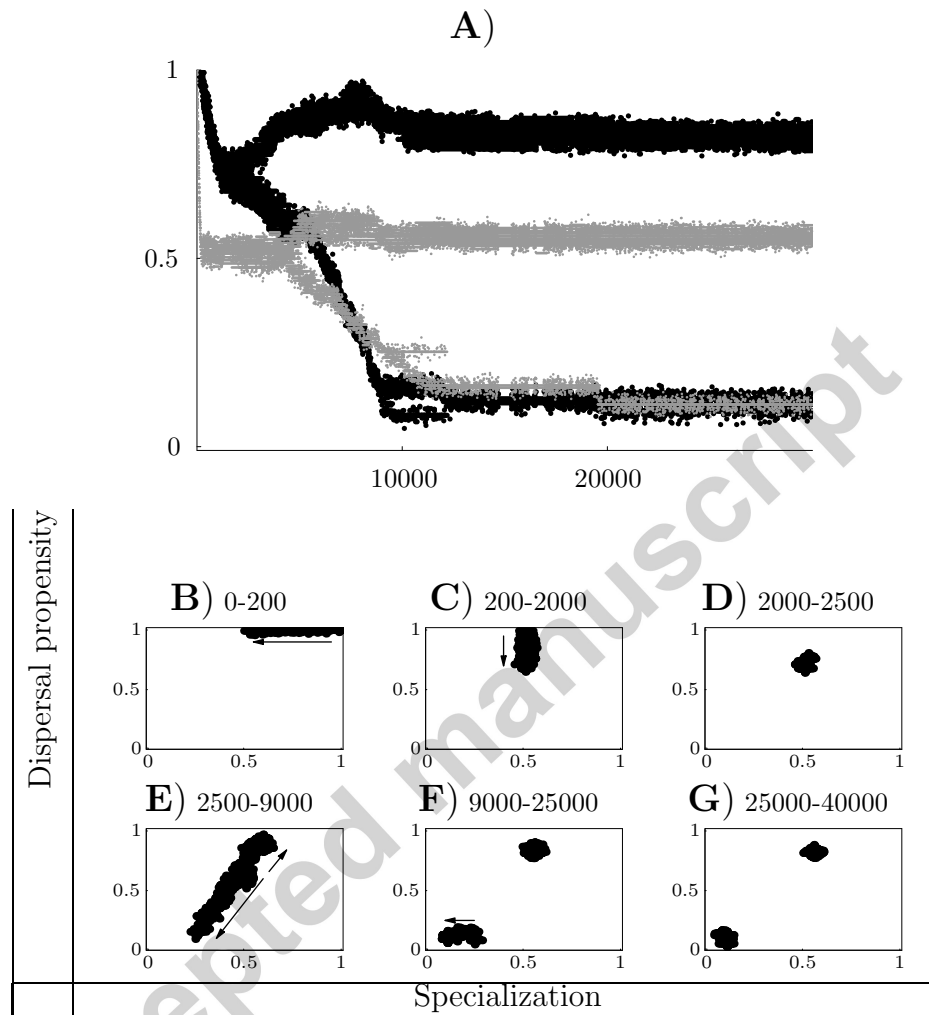


Figure 13: Panel A illustrates the strategies present in the metapopulation as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e . Each dot in Panels B-G represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s . The arrows in Panels B-G indicate the direction of evolution. The initial strategy $(e, s) = (1, 1)$. The simulation ended in a dimorphic population using strategies $(e, s) \approx (0.82, 0.55)$ and $(0.1, 0.09)$. Parameter values correspond to the ones in Figure 10F.

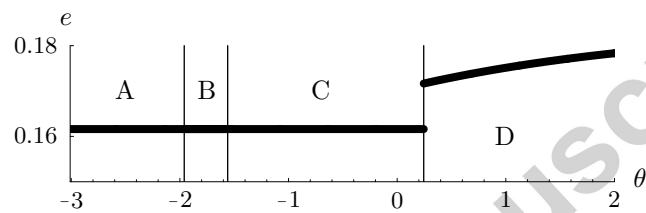


Figure 14: Evolutionarily singular dispersal propensity as a function of trade-off parameter θ . In area A, the evolution of specialization leads to a monomorphic specialist population (Figures 1A and 3A), whereas in area C, it ends in a dimorphic population employing the two fully specialized strategies (Figures 1E and 3C). In area B, the evolution of specialization leads to a population including either one or two of the specialists depending mainly on the initial state (Figures 1C and 5). In area D, the evolution of specialization leads to a generalist population (Figures 1I and 3D). Parameter values $c = 0.05$, $\pi = 0.8$, $\lambda = 3$, $K_1^1 = K_2^2 = 3$, $K_1^2 = K_2^1 = 1$ and $p_1 = p_2 = 0.5$ are the same as in the left column of Figure 1.

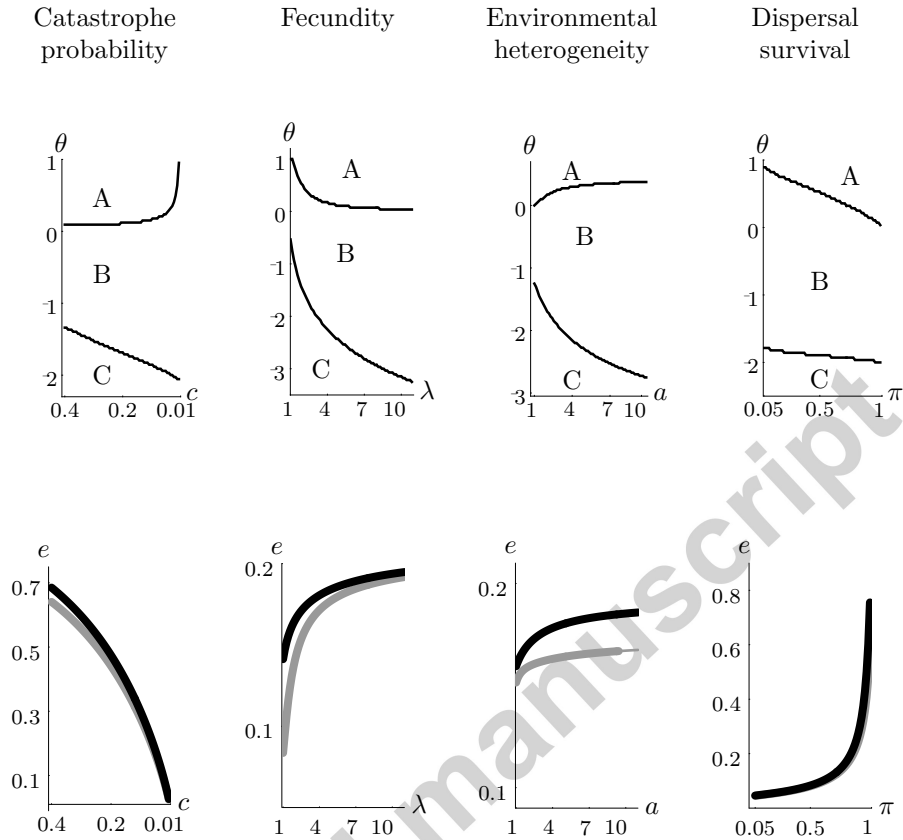


Figure 15: The panels in the upper row illustrate the critical values of the trade-off parameter θ as a function of different ecological parameters when dispersal propensity has the corresponding evolutionarily stable value. In area A, the generalist strategy is an evolutionary endpoint, in area B, it is a branching point and, in area C, it is an evolutionary repeller. The curve separating areas C and B stands for the critical value θ_1^* and the curve separating areas B and A stands for the critical value θ_2^* as a function of the parameter under consideration. The panels in the lower row illustrate the evolutionarily singular dispersal propensity as a function of different ecological parameters in a metapopulation consisting of generalist individuals ($\theta = 1$, black curve) and in a monomorphic metapopulation consisting of devoted specialists ($\theta = -3$, grey curve). The thick curve indicates that the singular strategy is an evolutionary endpoint, and thin curve indicates that evolutionary branching of dispersal may occur. In the analysis of the effect of environmental heterogeneity, we determine that $K_1^2 = K_2^1 = 1$ and $K_1^1 = K_2^2 = a$ and that a varies between 1 and 11. The parameters not under consideration as bifurcation parameters have the following values: $c = 0.05$, $\lambda = 3$, $K_1^1 = K_2^2 = 3$, $K_2^1 = K_1^2 = 1$, $p_1 = p_2 = 0.5$, $\pi = 0.8$.