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Live where you thrive: Joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity

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Live where you thrive:

Joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity

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ABSTRACT: We derive a comprehensive overview of specialization evolution based on analytical results and numerical illustrations. We study the separate and joint evolution of two critical facets of specialization local adaptation and habitat choice under different life cycles, modes of density regulation, and trade-off strengths. A particular feature of our analysis is the investigation of arbitrary trade-off functions. We find that local-adaptation evolution qualitatively changes the outcome of habitat-choice evolution under a wide range of conditions. In addition, habitat-choice evolution qualitatively and invariably changes the outcomes of local-adaptation evolution whenever trade-offs are weak. Even weak trade-offs, which favor generalists when habitat choice is fixed, select for specialists once local adaptation and habitat choice are both allowed to evolve. Unless trapped by maladaptive genetic constraints, joint evolution of local adaptation and habitat choice in the models analyzed here thus always leads to specialists, independent of life cycle, density regulation, and trade-off strength, thus raising the bar for evolutionarily sound explanations of generalism. Whether a single or two specialists evolve depends on the life cycle and the mode of density regulation. Finally, we explain why the gradual evolutionary emergence of coexisting specialists requires more restrictive conditions than their evolutionarily stable maintenance.

Ecological specialization is widely recognized as a major determinant of the emergence and maintenance of biodiversity (Futuyma and Moreno, 1988; Futuyma 1997; Maynard Smith 1989). It is therefore of crucial importance to understand the ultimate causes of ecological specialization, as well as the relationship between specialization and diversification. To this end, it is desirable to understand when evolution in heterogeneous environments leads to a single generalist, to a single specialist, or to the diversification and maintenance of several specialists and/or generalists.

Currently available theory offers quite a variety of models for the evolution of ecological specialization, each making different assumptions. Table 1 offers an extensive overview. Even though some factors have repeatedly been shown to be crucial for promoting or inhibiting specialization, their analysis within an integrative framework is as yet pending. Three of these factors are of particular importance. First, it is generally understood that for adaptation not to lead to a single all-purpose phenotype, which is the fittest in every habitat, one or more fitness trade-offs must exist (Levins 1968). Not surprisingly, the outcome of evolution has been shown to depend on the trade-off considered, with weaker trade-offs favoring generalists over specialists (e.g., Levins 1968; Brown 1990; van Tienderen 1991, 1997; Wilson and Yoshimura 1994; Sasaki and de Jong 1999; Kisdi 2001; Rueffler et al. 2004; Egas et al. 2004; Beltman and Metz 2005; Table 1).

Second, life-cycle characteristics have consistently been shown to affect the emergence and maintenance of local-adaptation polymorphisms in heterogeneous environments (seminal population genetics models were introduced by Levene 1953 and Dempster 1955; these were analyzed and compared by, e.g., Christiansen 1975; Karlin and Campbell 1981; Karlin 1982; Rausher 1984; Garcia-Dorado 1986, 1987; Hedrick 1990a; de Meeûs et al. 1993; van Tienderen 1997; Ravigné et al. 2004). In particular, local density regulation has been shown to generate frequency-dependent selection when acting on populations in habitats with different local allelic frequencies, thereby protecting local-adaptation polymorphisms (Ravigné et al. 2004). Population genetics simulation models (Diehl and Bush 1989; Fry 2003), adaptive dynamics models (Egas et al. 2004; Beltman and Metz 2005), as well as quantitative genetics models (Ronce and Kirkpatrick 2001) have confirmed that population dynamics, the timing of density regulation, and the spatial scale of density regulation (within or across habitats) are essential for the emergence and maintenance of local-adaptation polymorphisms (Table 1).

Third, it has generally been recognized that patterns of distribution of individuals among habitats strongly affect the outcome of selection for local adaptation. Specifically, both the emergence and the stable coexistence of locally specialized phenotypes are greatly facilitated by mechanisms of habitat choice that permit phenotypic segregation. Examples of such mechanisms are philopatry (e.g., Maynard Smith 1966; Brown and Pavlovic 1992; Meszéna et al. 1997; Geritz and Kisdi 2000; Kisdi 2002), learned habitat preference (e.g., Beltman et al. 2004; Beltman and Haccou 2005; Beltman and Metz 2005; Stamps and Davis 2006), and matching habitat choice (a preference of individuals for the habitat they are best adapted to; e.g., de Meeûs et al. 1993; Ravigné et al. 2004). Obviously, dispersal and habitat choice may themselves be subject to adaptive evolution (e.g., Fretwell and Lucas 1970; Doyle 1975; Ward 1987; Brown 1990; Fryxell 1997; see Jaenike 1990; Mayhew 1997; and Morris 2003 for reviews on habitat selection; see Ronce 2007 for a review on dispersal) and are thus expected to evolve jointly with local adaptation (de Meeûs et al. 1993; Rausher 1993; Table 1).

In this study we employ an integrative framework for investigating the gradual evolution of local adaptation and habitat choice in heterogeneous environments, with the aim of bridging across, and thereby unifying, a host of earlier more specialized studies. Our analysis simultaneously considers key ecological factors such as different life cycles, modes of density regulation, and trade-off shapes, as well as genetic factors such as the mutational or population-level trait variances and covariances. We study the separate evolution of local adaptation (performances) and habitat choice (preferences), as well as their joint evolution. Summarized in figure 1, our main results offer a synthetic overview, based on analytically derived conditions, of how outcomes of specialization evolution depend on the aforementioned key ecological factors. A particular feature of our analysis is the investigation of arbitrary trade-off functions, which implies that our results in this regard are as general as they can be. We also explore how conditions for the gradual emergence of specialization polymorphisms differ from those for their maintenance.

Methods

We consider a species that can inhabit two distinct habitats. Here the term habitat is understood in a general sense, as a subset of the environment exposing individuals to specific selection pressures (Morris 2003). Individuals are characterized by two traits: a local-adaptation trait that determines their performance within each habitat, and a habitat-choice trait that determines their propensity to settle in one habitat or the other. These traits naturally reflect two key facets of ecological specialization: the capacity for improved performance in a particular habitat, and the capacity for preferentially entering a particular habitat (Rausher 1984). We consider an asexual semelparous species with non-overlapping generations. All three life cycles described below imply that individuals experience selection in a single habitat during each reproductive season, and thus describe coarse-grained environments (Levins 1968; Morris 1992). We highlight that our model also applies to the particular case of an iteroparous species with discrete generations and survival and fecundities that are not age-specific. The reason is that surviving parents are then formally equivalent to one of their offspring. Iteroparous individuals can experience both habitats during their lifetime, so for them the models describe environments that are fine-grained at the time scale of generations and coarse-grained at the time scale of seasons.

Life cycles

Life cycles underlying the evolution of specialization in classical asexual dispersal-selection models comprise three steps: mixing and dispersal between two different habitats, selection within habitats, and density regulation. By definition of these models, selection is phenotype-dependent and density-independent, whereas density regulation is density-dependent and phenotype-independent. Density regulation may occur either separately within each habitat (local regulation) or jointly across habitats (global regulation). Whether dispersal occurs at the juvenile or the adult stage and whether selection concerns viability or fertility does not affect the structure, and thus the outcome, of these models.

As we have recently shown (Ravigné et al. 2004; see also Beltman et al. 2004), there are only three prototypical life cycles that can result from permuting these three steps. The first life cycle (hereafter called “Model 1”) was first described by Levene (1953) and is the most common model considered for analyzing soft selection (Wallace 1975). It is characterized by a periodic sequence of steps as follows:

1. Mixing and dispersal between two different habitats.
2. Selection within habitats.
3. Local density regulation within habitats.

As density regulation occurs locally after selection, habitat contributions to the next generation are independent of the phenotypic composition within a habitat (this is known as “constant habitat outputs” in dispersal-selection models of population genetics).

The second model ("Model 2") is the standard interpretation of a verbal model introduced by Dempster (1955). It is the most common model considered for analyzing hard selection, and is known to result in frequency-independent selection:

1. Mixing and dispersal between two different habitats.
2. Selection within habitats.
3. Global density regulation across habitats.

Here, as density regulation is global, habitat outputs depend on the phenotypic composition within habitats, and thus vary during the course of evolution (this is known as "variable habitat outputs" in dispersal-selection models of population genetics).

The regulation step may imply the gathering of all individuals in a third habitat in which density regulation takes place. For instance, the aphid *Pemphigus bursarius* (L.) feeds on lettuce roots during summer and can utilize two different habitats, soil and poplar trees, during winter (Phillips et al. 2000). If density is regulated on lettuce roots, regulation is global for traits involved in adaptation to the two winter habitats.

The last model ("Model 3"), combines local density regulation (as in Model 1) with variable habitat outputs (as in Model 2):

1. Mixing and dispersal between two different habitats.
2. Local density regulation within habitats.
3. Selection within habitats.

Model 3 (Ravigné et al. 2004) has not been considered traditionally. We have shown previously that Model 3 gives rise to frequency-independent selection (i.e., hard selection) when individuals distribute randomly among habitats, but causes frequency-dependent selection (i.e., soft selection) when they choose the habitat that they are best adapted to (Ravigné et al. 2004).

For Models 1 and 3, which imply local density regulation, C_1 and C_2 denote the local carrying capacities of habitats 1 and 2, respectively. For Model 2, which implies global density regulation, the global carrying capacity is chosen as $C_1 + C_2$. Local and global density regulations are based on a ceiling: only C_1 and C_2 or $C_1 + C_2$ individuals, respectively, survive the regulation step, independent of their phenotype. Habitats (Models 1 and 3) or the entire environment (Model 2) are thus assumed to be saturated after the regulation step. The relative carrying capacities of habitats 1 and 2 are denoted by $c_1 = C_1 / (C_1 + C_2)$ and $c_2 = 1 - c_1$, respectively.

It is worth pointing out that the question as to which of the three life cycles describes above best matches that of a particular organism can have different answers depending on which adaptive trait is at focus (Ravigné et al. 2004, Rueffler et al. 2006a, 2006b).

Dispersal and habitat choice

During the dispersal step at the beginning of each of the three life cycles, individuals settle in one habitat where they, or their offspring, experience natural selection. The distribution of individuals across habitats is determined by their habitat-choice trait h ($0 \le h \le 1$), measuring an individual's probability of settling in habitat 2 (accordingly, its probability of settling in habitat 1 is given by $1 - h$). In phytophagous insects, h may, for instance, represent the proportion of eggs laid by a female of phenotype h on a host plant of type 2, or the probability that emerging larvae choose to settle in habitat 2. Habitat choice is assumed to be genetically fixed without phenotypic plasticity.

Local adaptation and trade-offs

As a second adaptive trait, we consider a local-adaptation trait p ($0 \leq p \leq 1$) affecting the local fitnesses $w_1(p)$ and $w_2(p)$ in habitats 1 and 2, respectively. These local fitnesses only vary with the phenotype p and not with phenotypic frequencies. In phytophagous insects, p and $1-p$ may, for instance, describe the relative concentration of two enzymes that facilitate assimilation of nutrients from host plants of type 1 and 2 in the digestive tubes of larvae. Accordingly, $w_1(p)$ and $w_2(p)$ may characterize the survival of larvae feeding on host plants of type 1 or 2, respectively. Alternatively, $w_1(p)$ and $w_2(p)$ may be interpreted as the differential fecundities of adult females feeding on host plants of type 1 or 2, respectively.

Below we will mostly present analytical results that are valid for arbitrary functions $w_1(p)$ and $w_2(p)$. Following Spichtig and Kawecki (2004; see also HilleRisLambers and Dieckmann 2003; Egas et al. 2004), we will occasionally use two specific functions,

$$w_1(p) = 1 - sp^{\gamma} \tag{1a}$$

and

$$w_2(p) = 1 - s(1-p)^{\gamma} . \tag{1b}$$

for the sake of concreteness and the purpose of illustration. Here, the parameter γ determines the shape of the local fitness functions (see below), while the parameter s determines the maximum level of local maladaptation (the lowest possible local fitness is $1-s$, where $0 < s < 1$).

Terminology for describing trade-offs such as those defined by equations (1) is inhomogeneous in the literature. A first convention for characterizing convexity or concavity is based on the trade-off curve $w_2(w_1)$. The trade-off is described as convex if the second derivative of $w_2(w_1)$ is positive, and as concave otherwise. For the specific functions in equations (1), $\gamma < 1$ implies a convex trade-off and $\gamma > 1$ a concave trade-off. A second convention – used, for example, in the seminal analysis of trade-offs by Levins (1968) – is based on fitness sets. Fitness sets are defined as the sets of possible (observable) fitness combinations (w_1, w_2). These are thus delimited by the axes of the positive quadrant together with the trade-off curve $w_2(w_1)$. A fitness set is termed convex if any straight line connecting two fitness combinations within the set lies within the set (Levins 1968). Unfortunately, convex fitness sets are delimited by concave trade-off curves and vice versa, which can lead to confusion when referring to trade-offs as being convex or concave. To avoid any such confusion in this study, we adopt a third widely used convention throughout: hereafter we will refer to concave trade-off curves (and thus to convex fitness sets) as “weak trade-offs”, and to convex trade-off curves (and thus to concave fitness sets) as “strong trade-offs” (see the top row of figure 1 for illustrations). Under a weak trade-off between two components of fitness, increasing one of them only weakly reduces the other, whereas when the trade-off is strong this reduction is strong. For the specific functions in equations (1), $\gamma < 1$ implies a strong trade-off and $\gamma > 1$ a weak trade-off. Accordingly, trade-off strength in equations (1) can be measured by $1/\gamma$, and we thus refer to γ as the inverse trade-off strength.

Evolutionary dynamics

To investigate conditions facilitating the evolution of specialization, the local-adaptation trait p and the habitat-choice trait h are allowed to evolve. Outcomes of selection on these traits are examined using a generalized framework in which evolutionary rates are proportional to selection pressures. Two kinds of evolutionary dynamics are considered, which differ in their mathematical and biological underpinnings: one, in which the probability and size of mutations is assumed to be very small, so that evolution proceeds through the invasion and fixation of mutant phenotypes in otherwise monomorphic resident populations (as assumed in adaptive dynamics theory; Metz et al. 1992, 1996; Dieckmann and Law 1996; Geritz et al.

1997), and another, in which all phenotypes are present at all times, so that evolution proceeds by their differential growth in fully polymorphic resident populations (as assumed in quantitative genetics theory; Lande 1976; Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993). In first approximation, both kinds of dynamics give rise to evolutionary rates that are proportional to selection gradients (Iwasa et al. 1991; Dieckmann and Law 1996). The constant of proportionality involves the variance-covariance matrix either of the mutation distribution (in adaptive dynamics theory) or of the population distribution (in quantitative genetics theory). This formal equivalence allows our analysis to deal with both kinds of evolutionary dynamics at once.

Our analysis of evolutionary outcomes proceeds in three steps, which will be carried out below separately for the three fundamental life cycles described above. We begin by calculating invasion fitness, i.e., the long-term exponential growth rate of rare phenotypes (Metz et al. 1992). We then identify those (combinations of) trait values for which all selection pressures vanish. These are known as evolutionarily singular strategies and require that invasion fitness in each trait be at a local minimum or maximum (Metz et al. 1996; Geritz et al. 1997).

In a second step, we determine whether the identified singular strategies are convergence stable (CS, i.e., attainable through gradual evolution; Christiansen 1991) and/or locally evolutionarily stable (ES, i.e., situated at a local fitness maximum; Maynard Smith and Price 1973). These two stability properties are independent (Eshel and Motro 1981; Taylor 1989) and help distinguish between three different types of singular strategies of single-trait evolution: evolutionary end points known as continuously stable strategies (both CS and ES, resulting in stabilizing selection; Eshel and Motro 1981), evolutionary repellors (not CS, resulting in divergent selection; Metz et al. 1996), and evolutionary branching points (CS but not ES, resulting in disruptive selection; Metz et al. 1996). Phenotypic dimorphisms may emerge and be maintained at the latter type of singular strategy. This three-fold classification carries over from single-trait evolution to the joint evolution of two traits, except that an extra test is then needed for checking whether a protected dimorphism can exist close a singular strategy. For single-trait evolution this is guaranteed for any singular strategy that is CS but not ES (Dieckmann 1994; Geritz et al. 1997), whereas for joint evolution this property, known as mutual invasibility, has to be established separately for identifying evolutionary branching points.

As a third step, we consider the sensitivity of our results with respect to model parameters. The latter include c_1, as well as s and γ for the particular trade-offs considered in equations (1). When evolution occurs in only one trait, a fourth parameter is given by the non-evolving value of either h or p. Since all of these parameters are already dimensionless and affect dynamics separately, the number of essential parameters (either 3 or 4) cannot be further decreased. In addition, since the joint evolutionary dynamics of the two traits might depend on their variances and covariance (either mutational variances and covariance as in adaptive dynamics theory or population-level variances and covariance as in quantitative genetics theory), we also study the robustness of our results with respect to variation of these quantities.

Results

In this section we derive analytical expressions for the invasion fitness in each of the three life cycles and examine the resultant evolutionary dynamics of local adaptation and habitat choice – first separately and then jointly. On this basis, we explain the crucial differences between separate and joint evolution, investigate evolutionary bistabilities, and contrast conditions for the maintenance and gradual emergence of specialization polymorphisms.

Invasion fitnesses

When density regulation occurs locally after selection (Model 1), the invasion fitness of a variant with trait values $\tilde{p}$ and $\tilde{h}$ in a population with trait values p and h is

$$s_{p,h}(\tilde{p},\tilde{h}) = \ln\left(c_1 \frac{(1-\tilde{h})w_1(\tilde{p})}{(1-h)w_1(p)} + c_2 \frac{\tilde{h}w_2(\tilde{p})}{hw_2(p)} \right). \tag{2a}$$

When density regulation occurs globally (Model 2), the invasion fitness is

$$s_{p,h}(\tilde{p},\tilde{h}) = \ln\left(\frac{(1-\tilde{h})w_1(\tilde{p}) + \tilde{h}w_2(\tilde{p})}{(1-h)w_1(p) + hw_2(p)} \right). \tag{2b}$$

When density regulation occurs locally before selection (Model 3), the invasion fitness is

$$s_{p,h}(\tilde{p},\tilde{h}) = \ln\left(\frac{c_1 w_1(\tilde{p})}{c_1 w_1(p) + c_2 w_2(p)} \frac{1-\tilde{h}}{1-h} + \frac{c_2 w_2(\tilde{p})}{c_1 w_1(p) + c_2 w_2(p)} \frac{\tilde{h}}{h} \right). \tag{2c}$$

To illustrate the method of derivation, the invasion fitness in equation (2a) is deduced in Appendix A. In our model, p and h can be interpreted in two alternative ways. First, they may be viewed as the trait values of a monomorphic resident population, as in adaptive dynamics theory. Second, p and h can be interpreted as the population's mean trait values in a polymorphic resident population, as in quantitative genetics theory, assuming that the population-level variances of both traits around these means are small. Our analyses below are independent of which of these interpretations is preferred.

Evolution of local adaptation alone

We first analyze the evolution of local adaptation when habitat choice is fixed and monomorphic for some value of h (under passive and random dispersal, h, the probability of settling in habitat 2, is simply given by the frequency of habitat 2 in the environment, $h = c_2$). Results are summarized in figure 1 and proofs are given in Appendix B. Similar analyses were performed by Geritz et al. (1997), Kisdi and Geritz (1999; Model 1 for Gaussian local fitnesses), and Kisdi (2001; Model 1 for general local fitnesses). The qualitative conclusions reported in those earlier studies were similar to those derived here. In particular, most previous studies have emphasized the influence of trade-off strength on evolutionary outcomes, including models dealing with fine-grained environments (e.g., Rueffler et al. 2006b). Models 2 and 3 have not been considered previously in the form they are analyzed here. However, Meszéna et al. (1997), Egas et al. (2004; similar fitness functions but different density regulation), and Beltman and Metz (2005) examined life cycles that were similar to our Model 3.

Constant habitat outputs. For constant habitat outputs (local regulation after selection, Model 1), evolutionarily singular strategies p^* must satisfy

$$c_1 \frac{w_1'(p^*)}{w_1(p^*)} + c_2 \frac{w_2'(p^*)}{w_2(p^*)} = 0, \tag{3a}$$

with $w_i'(p) = dw_i(p)/dp$ for $i = 1, 2$. Evolutionarily singular strategies in Model 1 are therefore independent of habitat choice. If an evolutionarily singular strategy does not exist, selection always remains directional, so that the population will evolve an extreme degree of local adaptation ($p^* = 0$ or $p^* = 1$). If the trade-off is symmetric ($w_1(p) = w_2(1-p)$), and local carrying capacities are equal ($c_1 = c_2$), the generalist strategy $p^* = \frac{1}{2}$ is always singular (for the specific trade-offs given by equations (1) this is illustrated in fig. 2A). If carrying capacities differ, intermediate strategies other than $p^* = \frac{1}{2}$ may be singular (fig. 2B). For moderately strong trade-offs, the intermediate singular strategy is surrounded by two additional singular strategies (fig. 2A-B).

----- Figure 1 and Figure 2 near here -----

We now examine the properties of the evolutionarily singular strategies p^* in equation (3a). Results are summarized in figure 1. Singular strategies p^* in Model 1 are locally evolutionarily stable (ES) if

$$c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)} < 0 \tag{3b}$$

and convergence stable (CS) if

$$c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)} < c_1 \frac{w_1'(p^*)^2}{w_1(p^*)^2} + c_2 \frac{w_2'(p^*)^2}{w_2(p^*)^2} . \tag{3c}$$

with $w_i''(p) = d^2 w_i(p) / dp^2$ for $i = 1, 2$. The first inequality is fulfilled if the trade-off is weak at p^*, while the second one is fulfilled if the trade-off is weak or moderately strong at p^*. Thus, if the trade-off is weak at p^*, the singular strategy is both ES and CS: selection at p^* is stabilizing and p^* is an evolutionary end point (e.g., for the specific trade-offs given by equations (1) this is shown by thick curves in fig. 2A-B). The selected intermediate local-adaptation trait is then more or less generalist depending on relative carrying capacities (fig. 2A-B). If the trade-off is very strong at p^*, the singular strategy is neither ES nor CS: selection around p^* is divergent and p^* is an evolutionary repellor (dotted curves in fig. 2A-B). Selection then favors maximal adaptation to one habitat, depending on the initial trait value and relative carrying capacities. If the trade-off is only moderately strong at p^*, the intermediate singular strategy is CS but not ES: selection at p^* is disruptive and p^* is an evolutionary branching point (dashed curves in fig. 2A-B). In this case, an initial morph that is not too close to one of the specialists first converges toward p^* and then becomes dimorphic owing to the frequency-dependent disruptive selection experienced at p^*; the resultant two specialists subsequently evolve away from p^*. If one habitat has a much larger carrying capacity than the other, the range of trade-off strengths (as measured by $1/\gamma$) for which two coexisting specialists can evolve in this manner is reduced compared to the symmetric situation (compare fig. 2A and 2B).

It is worth highlighting that some trade-offs (such as those defined by equations (1)) imply the existence of three singular strategies. In such situations, evolutionary outcomes will depend on a population's initial level of local adaptation. As illustrated in figure 2A-B, with moderately strong trade-offs the intermediate branching point is then surrounded by two repellors. Consequently, a population that starts outside the range of local-adaptation traits delimited by the two repellors cannot reach the branching point through gradual evolution, and will instead maximally adapt to one habitat. In contrast, a population starting in between the two repellors will first evolve to the branching point and may then split into two coexisting specialists. For the specific trade-offs defined by equations (1), we corroborated that after evolutionary branching these two coexisting specialists become maximally adapted to either of the two habitats (results not shown). Contingent on the initial level of local adaptation, three qualitatively different evolutionary outcomes are thus possible.

Variable habitat outputs. With fixed habitat choice, life cycles with variable habitat outputs (Models 2 and 3) behave analogously to one another (for the specific trade-offs given by equations (1) this behavior is illustrated in fig. 2C-D), but rather differently from life cycles with constant habitat outputs (Model 1). Evolutionarily singular strategies p^* must satisfy the following equations, respectively, for global density regulation (Model 2) and for local density regulation (Model 3),

$$(1-h)w_1'(p^*)+hw_2'(p^*)=0\,, \tag{4a}$$

$$c_1w_1'(p^*)+c_2w_2'(p^*)=0\,. \tag{4b}$$

The singular strategy thus only depends on the distribution of individuals at the time of selection (described by $1-h$ and h in Model 2, and by c_1 and c_2 in Model 3) and on the local trade-off shape (described by $w_1'(p^*)$ and $w_2'(p^*)$). If both habitats have the same population size when selection occurs (i.e., if they are equally visited in Model 2, $1-h=h$, or if they have the same carrying capacity in Model 3, $c_1=c_2$), strategies p^* with $w_1'(p^*)=-w_2'(p^*)$ are singular. If the trade-off is symmetric ($w_1(p)=w_2(1-p)$) and the local fitness functions are either convex or concave, the latter condition is only fulfilled at $p^*=\frac{1}{2}$. For instance, for the specific trade-offs given by equations (1), in Model 2 the singular strategy (fig. 2C-D) is given by

$$p^*=\frac{1}{1+\sqrt[\gamma-1]{h^{-1}-1}}. \tag{4c}$$

We can see that $h=\frac{1}{2}$ implies $p^*=\frac{1}{2}$, independent of the trade-off strength $1/\gamma$ (fig. 2C). In Model 3, the singular strategy (fig. 2C-D) is similarly given by

$$p^*=\frac{1}{1+\sqrt[\gamma-1]{c_2^{-1}-1}}. \tag{4d}$$

Analogously, $c_2=\frac{1}{2}$ implies $p^*=\frac{1}{2}$, independent of the trade-off strength $1/\gamma$ (fig. 2C).

We return to general trade-off functions and examine the properties of the evolutionarily singular strategies p^* in equations (4a) and (4b). If the trade-off is strong at p^*, p^* is a repellor (neither ES nor CS; eqq. [B7/B8] and [B11/B12] are not fulfilled). In this case, the population maximally adapts to one habitat or the other, depending on the initial trait value and relative carrying capacities. If the trade-off is weak at p^*, p^* is an evolutionary end point (both CS and ES; eqq. [B7/B8] and [B11/B12] are fulfilled). The selected local-adaptation trait p^* will then be intermediate between the two extreme specialists. Equations (4) show that this intermediate phenotype is tuned by habitat contributions to the next generation (i.e., according to relative population sizes just before mixing) if density regulation is local (Model 3), whereas it depends on habitat choice if density regulation is global (Model

2). It thus corresponds to a strategy that is equally well adapted to both habitats (fig. 2C) only when those are of similar quality under local density regulation (Model 3) or are visited in equivalent frequencies under global density regulation (Model 2). When one habitat is visited more frequently than the other under global density regulation (Model 2), or when it possesses a larger carrying capacity than the other under local density regulation (Model 3), evolution thus often favors local adaptation biased toward this habitat, irrespective of trade-off shape (fig. 2D).

Evolution of habitat choice alone

We now assume that every individual in the population has the same fixed and non-evolving level of local adaptation p. Results are summarized in figure 1 and proofs are given in Appendix C. Conclusions reported in this section can be found in classical studies on the evolution of habitat choice (e.g., Fretwell and Lucas 1970; Rosenzweig 1981).

With constant habitat outputs (Model 1), the only singular strategy for habitat choice h is CS and ES (or, more precisely, neutrally ES, see Appendix C),

$$h^* = c_2 . \tag{5a}$$

With variable habitat outputs due to global regulation (Model 2), habitat choice h is selectively neutral if p is such that $w_1(p) = w_2(p)$. Otherwise, selection is directional and favors maximal preference for the more favorable habitat,

$$h = 0 \text{ or } h = 1. \tag{5b}$$

With variable habitat outputs due to local regulation before selection (Model 3), the only singular strategy for h is CS and ES,

$$h^* = \frac{c_2 w_2(p)}{c_1 w_1(p) + c_2 w_2(p)} . \tag{5c}$$

In life cycles with local density regulation (Models 1 and 3), the selected strategy is an "opportunist" (Rosenzweig 1981): individuals distribute themselves according to habitat productivities (i.e., according to local population sizes before mixing). Hence, the intensity of competition is the same in both habitats, implying an ideal free distribution (Fretwell and Lucas 1970; Fretwell 1972; Rosenzweig 1981; Morris 1988). In contrast, when density regulation is global, the selected strategy exhibits extreme "pickiness" (Rosenzweig 1981).

Joint evolution of local adaptation and habitat choice

We now examine the general situation in which local adaptation and habitat choice evolve jointly. Results are summarized in figure 1 and proofs are given in Appendix D.

With constant habitat outputs (local regulation after selection, Model 1), the singular strategy (p^*, h^*) determined by equations (3a) and (5a) is intermediate. It is not ES (eq. [D23]). When the trade-off is sufficiently strong, the singular strategy is an evolutionary saddle point (i.e., it attracts the evolutionary dynamics in the two-dimensional trait space in one direction, but repels in another direction; fig. 3A). In contrast, when the trade-off is weak or moderately strong (fig. 3D; eq. [5]), the singular strategy is convergence stable, irrespective of the genetic variance-covariance structure of p and h (eq. [D12]). It is then an evolutionary branching point (i.e., a point in the vicinity of which a dimorphism can emerge; fig. 3D), unless the two traits are strongly negatively correlated (so that the two strategies that would naturally diverge from the singular strategy cannot coexist; Appendix D). We have thus shown that in Model 1, under the assumptions considered here, joint evolution cannot result in a generalist unless maladaptive genetic constraints trap the population at the singular point.

With variable habitat outputs due to global regulation (Model 2), the singular strategy (p^*, h^*), if it exists (eq. [D4]), is always an evolutionary saddle point (fig. 3C; eq. [D14]), irrespective of the variance-covariance structure. Independent of trade-off shape, selection favors a picky specialist that is completely adapted to one habitat and consistently chooses it, leaving the other habitat empty.

With variable habitat outputs due to local regulation before selection (Model 3), the singular strategy (p^*, h^*) is given by equations (4b) and (5c) (with $p = p^*$). It is never ES (eq. [D24]). If the trade-off is strong (eq. [D18] not fulfilled), (p^*, h^*) is an evolutionary saddle point (fig. 3B), irrespective of the variance-covariance structure. If the trade-off is very weak (eq. [D20]), (p^*, h^*) is an evolutionary branching point, unless the two traits are strongly negatively correlated (so that the two strategies that naturally diverge from the singular strategy cannot coexist; Appendix D). If the trade-off is moderately weak, the variance-covariance structure determines whether the singular point is CS (making it a branching point) or not (making it a repellor): the singular point then is CS unless the covariance between p and h is positive and larger than a threshold that rises for trade-offs that are increasingly weak (eq. [D21]).

Regarding the impact of genetic variances and covariances on the outcomes of joint evolution, we can thus conclude that, in general, the outcome of gradual evolution is independent of the relative genetic variances of, and the genetic covariance between, the local-adaptation trait and the habitat-choice trait. Depending on the evolutionary dynamics considered, this conclusion applies either to the population-level variance-covariance structure in the quantitative genetics approach or to the mutational variance-covariance structure in the adaptive dynamics approach. This conclusion does not apply only when strongly negatively correlated traits are combined with weak to moderately strong trade-offs in Model 1 or with weak trade-offs in Model 3, or when strongly positively correlated traits are combined with moderately weak trade-offs in Model 3 (Appendix D).

----- Figure 3 near here -----

Comparison of evolutionary dynamics and outcomes

We now summarize conditions for the gradual emergence of polymorphism under the joint evolution of habitat choice and local adaptation. When the trade-off is weak, polymorphisms can emerge if density regulation is local, independent of whether this regulation leads to variable habitat outputs (Model 3) or to constant habitat outputs (Model 1); global regulation then precludes polymorphism. Conversely, when the trade-off is strong, variable habitat outputs preclude the emergence of polymorphisms, both in Model 2 (local regulation before selection) and in Model 3 (global regulation); polymorphism can then only emerge if local regulation occurs after selection (Model 1) and the trade-off is not too strong.

We have shown that in all three prototypical dispersal-selection models the joint evolution of habitat choice and local adaptation leads to outcomes that qualitatively differ from those obtained for single-trait evolution as soon as local-adaptation trade-offs are weak (gray area in fig. 1). In particular, and perhaps most unexpectedly from a traditional perspective, under joint evolution weak trade-offs never select for generalists, but instead always favor specialization. Whether or not such specialization is then associated with diversification depends on the life cycle, with local regulation enabling diversification.

Geometrical interpretation of analytical results

To interpret the differences between single-trait and two-trait evolution and to understand more generally how trade-offs in our models affect singular strategies and their properties, we employ a geometrical analysis (de Mazancourt and Dieckmann 2004; Rueffler et al. 2004) that generalizes the classical fitness-set approach introduced by Levins (1968) to systems with frequency-dependent selection. The method is based on plotting trade-off functions together with invasion boundaries for the singular strategy being the resident strategy (fig. 4). For each resident strategy (w_1, w_2, h) (not constrained by the trade-off, so that w_1 and w_2 are independent), the invasion boundary is defined by the set of variant strategies $(\hat{w}_1, \hat{w}_2, \hat{h})$ that have the same invasion fitness as the resident. We focus the geometrical illustrations below on Model 1, since it was this life cycle that exhibited the most dramatic differences between single-trait and two-trait evolution (fig. 1A and 1C).

When habitat choice is fixed and local adaptation evolves alone, the invasion boundary lies in the two-dimensional space defined by the two local fitnesses (fig. 4A-B). This invasion boundary is linear for all residents and life cycles (fig. 4A-B; eqq. [E2-E4]). Figure 4A shows geometrically why in this case a weak trade-off can only induce evolutionarily stable strategies (either evolutionary end points or Garden-of-Eden configurations; Hofbauer and Sigmund 1990; Dieckmann 1997; Rueffler et al. 2004; de Mazancourt and Dieckmann 2004): when the singular local-adaptation trait is resident, resulting in the resident strategy $(w_1(p^*), w_2(p^*))$, all other trait combinations $(\hat{w}_1, \hat{w}_2)$ along the trade-off curve $w_2(w_1)$ have negative invasion fitness, so that evolution must come to a halt there. This confirms our analytical results for single-trait evolution (fig. 1A).

When allowing for two-trait evolution, in contrast, we can see geometrically that weak trade-offs lead to evolutionary branching points. In this case, the invasion boundary is a curved surface in the three-dimensional space defined by the two local fitnesses and the habitat-choice trait (fig. 4C). The singular local-adaptation trait, which was not invasible under single-trait evolution, now becomes invasible by morphs that differ consistently from it in both their habitat-choice trait and their local-adaptation trait: relative to the singular morph, such morphs have an elevated preference for the habitat in which they perform better. Geometrically, this invasibility is visible through the corresponding part of the trade-off surface lying above the invasion boundary, thus extending into the region of positive invasion fitness (fig. 4C). The resultant fitness landscape evidences disruptive selection (fig. 4E).

We provide analogous illustrations for a moderately strong trade-off (fig. 4B, 4D, and 4F). While for two-trait evolution the situation is similar to that for a weak trade-off (compare fig. 4D with fig. 4C and fig. 4F with fig. 4E), a salient difference occurs for single-trait evolution (compare fig. 4B with fig. 4A): now, when the singular local-adaptation trait is resident, all other trait combinations $(\hat{w}_1, \hat{w}_2)$ along the trade-off curve $w_2(w_1)$ have positive invasion fitness, so that evolutionary branching can occur even when habitat choice is fixed.

----- Figure 4 near here -----

Evolutionary bistability

The analysis above reveals that sufficiently strong trade-offs and global density regulation, either separately or jointly, result in divergent selection on local adaptation (fig. 1A and 1C). This favors maximal adaptation to one habitat and, if habitat choice also evolves, maximal preference to the same habitat. In such situations, the two specialist phenotypes are alternative evolutionary end points, a situation that is best described as evolutionary bistability (fig. 1). It is then desirable to predict which habitat a given population will ultimately specialize on.

When habitat choice is fixed, evolutionary bistability occurs as summarized in figure 1A. The outcome of local-adaptation evolution then depends on the population’s initial local-adaptation trait, and the basins of attraction of the two extreme specialist phenotypes are separated by evolutionary repellors (dotted curves in fig. 2). These basin boundaries may change with the strength of the trade-off (fig. 2A, 2B, and 2D), as well as with the relative habitat carrying capacities in life cycles with local regulation (Models 1 and 3; eqq. [3a] and

[4b] respectively; fig. 2B and 2D respectively) or the relative habitat preferences in life cycles with global regulation (Model 2; eq. [4a]; fig. 2D).

When habitat choice evolves jointly with local adaptation, evolutionary bistability occurs as summarized in figure 1C. Bistability is then associated with an evolutionary saddle point, with this point's stable manifold serving as the separatrix (dotted curves in fig. 3) between the basins of the two alternative evolutionary attractors. In general, the orientation and shape of this separatrix will be affected by the population-level variance-covariance structure (quantitative genetics approach) or by the mutational variance-covariance structure (adaptive dynamics approach) of the two considered traits. Assuming genetic independence of habitat choice and local adaptation evolution, so that the genetic covariance between these traits vanishes, allows us to distinguish two qualitatively different cases. When regulation is local (Models 1 and 3), initial habitat choice does not affect the evolutionary outcome (vertical separatrices in fig. 3A and 3B) and the initial local-adaptation trait then matters just as when habitat choice is fixed. In contrast, when regulation is global (Model 2), the initial values of both traits jointly affect the evolutionary outcome (slanted separatrix in fig. 3C) and the slope of the separatrix varies with trade-off strength (fig. 3E). Specifically, when the trade-off is weak (high γ), the separatrix is less steep, so that the evolutionary outcome depends more sensitively on initial habitat choice than on initial local adaptation.

Maintenance and gradual emergence of coexisting specialists

Our analysis so far has determined conditions for the emergence of polymorphisms through gradual evolution. Classical population genetics models (e.g., Levene 1953; Dempster 1955; Maynard Smith 1966; Templeton and Rothman 1981; Beltman et al. 2004; Ravigné et al. 2004; model type 1 in Table 1) instead focused on conditions for the maintenance of polymorphisms.

A polymorphism is called protected, and can thus be maintained against demographic perturbations, if all its members can reinvade after their disappearance (Prout 1968). For instance, under random dispersal, it is easily shown that with constant habitat outputs (Model 1) and with fitnesses defined by equations 1, a polymorphism of two extreme specialists $p_1 = 0$ and $p_2 = 1$ is protected if

$$\frac{1-s}{2-s} < c_1, c_2 < \frac{1}{2-s}. \qquad (6)$$

This leads to two conclusions (fig. 5, upper left panel). First, a polymorphism between the two specialists is protected in Model 1 if the carrying capacities of the two habitats are not too different and if the maximum level s of local maladaptation is large enough. Second, whether such a polymorphism is protected is independent of the curvature of the trade-off function, as the latter only affects intermediate morphs. In contrast, our results above have shown how the curvature of a trade-off function restricts the conditions under which a polymorphism can emerge through gradual evolution (fig. 1-4). The conditions for the protection of a polymorphism are thus wider than those for its emergence through gradual evolution (fig. 5).

Therefore, mutations or recombinations of particularly large phenotypic effect, or the immigration of non-resident strategies from the outside, can facilitate the emergence of specialization polymorphisms. When a polymorphism of two specialists cannot emerge through gradual evolution, but can be maintained once it has emerged, it may or may not be immune against the invasion of intermediate strategies depending on the considered trade-off strength. For instance, with constant habitat outputs (Model 1) and fixed random dispersal, a protected dimorphism of specialists is globally evolutionarily stable if and only if the trade-off is strong (Appendix B). In contrast, when the trade-off is weak, any intermediate strategy can invade (Appendix B). This is different under matching habitat choice (*sensu* Ravigné et al. 2004): protected dimorphisms of specialists are then always globally evolutionarily stable, irrespective of habitat outputs and trade-off strength (Appendix B).

----- Figure 5 near here -----

Discussion

Local adaptation and habitat choice have long been recognized as two critical facets of ecological specialization (Rosenzweig 1981). Yet, few theoretical studies have explicitly addressed their joint evolution (Castillo-Chavez et al. 1988; de Meeûs et al. 1993; Beltman and Haccou 2005; Beltman and Metz 2005; Rueffler et al. 2007; Table 1). Here we have introduced a simple integrative framework that enabled us to study analytically the separate and joint evolution of these two traits under different life cycles, modes of density regulation, and arbitrary trade-off shapes. Below, we summarize our main findings and discuss them in the wider context of past and future research.

Joint evolution qualitatively changes the specialization process

Central results of our study concern the conditions under which, relative to separate evolution, the joint evolution of local adaptation and habitat choice critically alters the specialization process (fig. 1).

We find that only very strong trade-offs prevent the outcomes of joint evolution from differing qualitatively from those of single-trait evolution. In other words, under very strong trade-offs, outcomes of joint evolution can be understood simply as the superposition of outcomes of single-trait evolution. Indeed, very strong trade-offs always favor i) maximal local adaptation to one habitat, and ii) either maximal preference for that habitat (when density regulation occurs globally across habitats) or an ideal free distribution across habitats (when density regulation occurs locally within habitats). This is because under very strong trade-offs the singular strategy (usually an intermediate adaptation trait value) is an evolutionary repellor. Even when habitat choice evolves jointly with local adaptation, gradual adaptive evolution can only diverge from this singular point, thereby leading to complete specialization on one habitat.

Habitat-choice evolution can qualitatively change local-adaptation evolution (shaded area in fig. 1C). This occurs for weak trade-offs, which always favor generalists when habitat choice is fixed (e.g., Levins 1962, 1968; MacArthur and Levins 1964; MacArthur and Pianka 1966; Lawlor and Maynard Smith 1976; Wilson and Turelli 1986; Van Tienderen 1991; Kisdi and Geritz 1999; fig. 1A), but select for specialists once habitat choice is allowed to evolve jointly with local adaptation (fig. 1C). A corresponding result was established by Rueffler et al. (2007) in a quite different model.

Similarly, local-adaptation evolution can qualitatively change habitat-choice evolution (hatched area in fig. 1C). This occurs when density regulation is local, which under fixed local adaptation always favors intermediate habitat choice, and thus leads to an ideal free distribution across habitats (Doyle 1975; Fryxell 1997; Fretwell 1972; Fretwell and Lucas 1970; Rausher 1984; fig. 1B). In contrast, the joint evolution of local adaptation and habitat choice under local density regulation can yield coexisting specialists, each with a maximal preference for the matching habitat (fig. 1C).

Evolution of habitat choice may leave habitats empty

A particularly surprising outcome of evolution of habitat choice occurs when density regulation is global (Model 2, often regarded as the prototypical model of hard selection; Dempster 1955). Selection then always favors the emergence of a single specialist, irrespective of whether or not local adaptation evolves together with habitat choice. Under joint evolution, this specialist is maximally adapted to one habitat and exhibits maximal preference for it. To the extent that habitat choice is accurate, this evolutionary outcome will leave the other habitat essentially empty. This extends a result of former theoretical studies: even with matching habitat choice, local-adaptation polymorphisms cannot be maintained under hard selection (de Meeûs et al. 1993; Ravigné et al. 2004). Furthermore, even when local adaptation is fixed and only habitat choice evolves, evolution under global density regulation leads to the exploitation of only a single niche.

These considerations could explain why some host plants are not utilized by some herbivorous insects, even though the plants are suitable for the insects' survival and reproduction (e.g., Smiley 1978; Rhode 1979; Myers et al. 1981; Anderson et al. 1989). The explanation has two components. First, our analyses predict that under global regulation habitat preference will evolve to be maximal: regulation being global, there is no benefit in exploiting the less crowded and/or productive habitat. Each genotype is in competition with every other genotype in the whole population. It is therefore evolutionarily advantageous for the focal herbivore species to concentrate its habitat preference on the habitat to which it is adapted, even at the expense of leaving the other habitat unexploited. Second, and for the same reason, an immigrating herbivore species that enters the empty habitat and is capable of exploiting it, without, however, already possessing maximal habitat preference for that empty habitat, will be competitively excluded by the focal herbivore species (e.g., de Meeûs et al. 1993). Owing to global regulation, the empty habitat will thus remain (almost) empty even in the face of joint evolution and immigration attempts. Under local regulation, evolutionary bistability also leads to a single specialist, but when habitat choice evolves, this specialist occurs in both habitats in an ideal free distribution (fig. 1C).

Joint evolution resolves the "soft selection/hard selection dilemma"

The so-called "soft selection/hard selection dilemma" was put forward in the context of population genetics models of resource specialization (de Meeûs 2000). The dilemma arises from recognizing that the evolution of coexisting picky specialists could be difficult, since specialization in habitat choice and local adaptation, when viewed as separate processes, require different ecological settings to evolve. Specifically, for fixed and monomorphic local adaptation, matching habitat choice only evolves either under hard selection (Model 2; Garcia-Dorado 1987; de Meeûs et al. 1993; fig. 1B) or in the presence of a pre-existing local-adaptation polymorphism (leading to the well-known "ghost of competition past"; Lawlor and Maynard Smith 1976; Rosenzweig 1981; Garcia-Dorado 1987; Castillo-Chavez et al. 1988; Brown and Pavlovic 1992; de Meeûs et al. 1993; Morris 1999). In contrast, for fixed and unconditional habitat choice, local-adaptation polymorphisms can only be protected under soft selection (Model 1; fig. 1A) and even then only evolve under restrictive conditions (Levene 1953; Ravigné et al. 2004; fig. 5).

Our analyses above have shown that, when habitat choice and local adaptation evolve jointly, the soft selection/hard selection dilemma is overcome: joint evolution leads to coexisting picky specialists under a much wider range of conditions (fig. 1C) than is expected from the mere superposition of results of separate evolution (fig. 1A-B). In particular, joint evolution allows maximal habitat preferences to evolve even under local regulation, thus eliminating the previously perceived discrepancy with requirements for local-adaptation polymorphisms.

Joint evolution raises the bar for understanding the evolution of generalists

For the entire range of models studied here, joint evolution precludes the emergence of generalists. Consequently, the classical, and still widely touted, view that weak trade-offs favor generalists (Levins 1968) can no longer be regarded as being adequate.

Our study has shown that the evolution of generalists can only be explained by additional factors that are not part of our models. Previous theoretical studies have suggested several such additional factors. First and foremost is temporal variability in habitat quality, which has long been recognized as favoring generalists (reviewed by Wilson and Yoshimura 1994; see also Kisdi 2002; Egas et al. 2004; Abrams 2006a). Fluctuating environments select for mean geometric reproductive success, so that specialists that recurrently experience poor performance in the habitat to which they are adapted are intrinsically disadvantaged. However, when fluctuations are fast, the trade-off curves examined in this study can simply be interpreted in terms of mean geometric reproductive success, or long-term fitness, instead of in terms of immediate performance, or instantaneous fitness. Our analyses then directly carry over to fluctuating environments.

Second, any ecological factor obstructing the evolution of a matching habitat choice will favor generalist local-adaptation strategies. Such constraints may originate from selective pressures that favor dispersal (e.g., kin competition; Ronce et al. 2001; Ronce 2007) and thus indirectly select against matching habitat choice (*sensu* Ravigné et al. 2004; see also Edelaar et al. 2008). Constraints on matching habitat choice may also arise from physiological limits to choice accuracy that result from errors in perception or implementation (Egas et al. 2004), or from costs associated with lengthy decision taking (“neural constraint”; Bernays 1998; see Mayhew 1997; Morris 2003 for reviews). Similarly, the time and effort required for sampling possibly rare candidate habitats (Jaenike 1990; Mayhew 1997) may favor generalism (Rosenzweig 1974; Rueffler et al. 2007).

Third, generalist species may persist as a result of genetic constraints. Even when selection favors the emergence of specialists, the segregation and recombination implied by sexual reproduction (with local-adaptation traits determined by multiple loci without extreme linkage or epistasis, or by diploid inheritance without full dominance) may impede specialization by constantly creating hybrids between the two specialist phenotypes (Felsenstein 1981; Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000). In this manner, frequency-dependent disruptive selection may trap populations at fitness minima (Dieckmann et al. 2004a, 2004b). If this phenomenon were significant in nature, generalists might be more frequent among sexual species than among asexual and selfing species. Moreover, theoretical studies suggest that sexual species are more likely to escape such fitness traps by so-called “one-allele mechanisms” (Felsenstein 1981; Dieckmann and Doebeli 1999, 2004), which apply when matching habitat preferences are based, for example, on philopatry or learned habitat preference (e.g., Brown and Pavlovic 1992; Kisdi and Geritz 1999; Day 2001; Beltman and Metz 2005). It is thus conceivable that one-allele mechanisms of habitat choice are relatively more common among recently evolved sexual specialists.

Joint evolution still needs to be understood under more complex types of density regulation

A common feature of the three models analyzed here is that population dynamics were kept as simple as possible. Specifically, density regulation was assumed to occur at a particular time in the life cycle and ensured that at most $C_1 + C_2$ individuals survived. This assumption is in line with most previous models of hard and soft selection, and probably is the main prerequisite that allowed us to obtain analytical results (unlike, e.g., Beltman and Metz 2005).

Naturally, it would be worthwhile to investigate the sensitivity of specialization evolution to more complex population dynamics. In many models incorporating such dynamics, the population is density-regulated using logistic functions (Egas et al. 2004) or Beverton-Holt functions (Kisdi 2002; Beltman and Metz 2005). A careful comparison between our results and evolutionary outcomes in those other models leads to the following two conclusions. First, when local carrying capacities underlying more realistic types of density regulation are assumed to be unaffected by local-adaptation traits, then Model 1 correctly predicts, depending on the strength of the trade-off, whether the generalist singular strategy is an evolutionary end point, a branching point, or a repellor. Second, when such local carrying capacities are assumed to change as local adaptation evolves (e.g., Egas et al. 2004), then our Model 3 correctly predicts the evolutionary outcomes, again in dependence of the assumed trade-off. These conclusions suggest that the three models investigated in this study, simple as they may be, might indeed be good approximations of models with more complex types of density regulation. Future theoretical work on the interactions between population dynamics and local adaptation could examine how far these approximations can be taken.

This study has shown how three key determinants of specialization evolution – the spatial scale of density regulation, the dependence of carrying capacities on local-adaptation traits, and the shape of local-adaptation trade-offs – can be integrated into a synthetic framework. This allowed us to derive analytical results on how the joint dynamics of local adaptation and habitat choice is crucial for understanding specialization evolution. We hope that theoretical and empirical studies will soon critically evaluate the generality of findings presented here.

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APPENDIX: ANALYTICAL PROOFS

A – Invasion fitnesses

Here we detail the calculation of invasion fitness for Model 1; calculations for Models 2 and 3 proceed analogously. We consider the following processes in the life cycle of an asexual population: dispersal, selection, regulation, and mixing. At the beginning of each cycle, individuals are part of a common pool with $N(t)$ residents and a small number $\tilde{N}(t)$ of variants. They first distribute across the two habitats according to their habitat-choice trait. After this stage, habitat 1 thus contains $(1-\tilde{h})\tilde{N}(t)$ variants and $(1-h)N(t)$ residents, while habitat 2 contains $\tilde{h}\tilde{N}(t)$ variants and $hN(t)$ residents. Selection occurs as individuals differentially reproduce and/or survive in each habitat according to their local adaptation trait. After this stage, there are thus $(1-\tilde{h})\tilde{N}(t)w_1(\tilde{p})$ variants and $(1-h)N(t)w_1(p)$ residents in habitat 1, and $\tilde{h}\tilde{N}(t)w_2(\tilde{p})$ variants and $hN(t)w_2(p)$ residents in habitat 2. Regulation occurs next: only a fixed number of individuals survive in each habitat; this number is independent of their strategy. After this stage, the variant population is given by

$$\tilde{N}_1(t) = C_1 \frac{(1-\tilde{h})\tilde{N}(t)w_1(\tilde{p})}{(1-h)N(t)w_1(p) + (1-\tilde{h})\tilde{N}(t)w_1(\tilde{p})} \tag{A1}$$

in habitat 1 and by

$$\tilde{N}_2(t) = C_2 \frac{\tilde{h}\tilde{N}(t)w_2(\tilde{p})}{hN(t)w_2(p) + \tilde{h}\tilde{N}(t)w_2(\tilde{p})} \tag{A2}$$

in habitat 2. From one cycle to the next, the variant's total population size thus changes according to

$$\tilde{N}(t+1) = \tilde{N}_1(t) + \tilde{N}_2(t)\,. \tag{A3}$$

Assuming that the variant population is small relative to the resident population, so that $N(t) \approx C_1 + C_2$, allows us to simplify this result, which gives

$$\tilde{N}(t+1) \approx \left(\frac{C_1}{C_1+C_2} \frac{(1-\tilde{h})w_1(\tilde{p})}{(1-h)w_1(p)} + \frac{C_2}{C_1+C_2} \frac{\tilde{h}w_2(\tilde{p})}{hw_2(p)} \right) \tilde{N}(t) . \tag{A4}$$

Hence, we obtain the variant's invasion fitness in Model 1 as

$$s_{p,h}(\tilde{p},\tilde{h}) = \ln\left(c_1 \frac{(1-\tilde{h})w_1(\tilde{p})}{(1-h)w_1(p)} + c_2 \frac{\tilde{h}w_2(\tilde{p})}{hw_2(p)} \right), \tag{A5}$$

thus recovering equation (2a).

B – Evolution of local adaptation alone

Selection gradients and singular strategies

The selection gradient is defined as the derivative of invasion fitness taken with respect to the variant strategy and evaluated at the resident strategy,

$$D_p(p,h) = \left(\frac{\partial s_{p,h}(\tilde{p},h)}{\partial \tilde{p}} \right)_{\tilde{p}=p} . \tag{B1}$$

For Model 1, we obtain

$$D_p(p,h) = c_1 \frac{w_1'(p)}{w_1(p)} + c_2 \frac{w_2'(p)}{w_2(p)} . \tag{B2}$$

For Model 2, we obtain

$$D_p(p,h) = \frac{(1-h)w_1'(p) + hw_2'(p)}{(1-h)w_1(p) + hw_2(p)} . \tag{B3}$$

For Model 3, we obtain

$$D_p(p,h) = \frac{c_1 w_1'(p) + c_2 w_2'(p)}{c_1 w_1(p) + c_2 w_2(p)} . \tag{B4}$$

A strategy is singular if its selection gradient vanishes. Hence in all three models, if a singular local-adaptation trait p^* exists, $w_1'(p^*)$ and $w_2'(p^*)$ either have opposite signs (i.e., there is a trade-off in local adaptation) or both vanish (i.e., p^* is optimal in both habitats). If a singular local-adaptation trait does not exist, the selection gradient never vanishes, and selection then always remains directional. For the remainder of the appendix, we focus on cases characterized by trade-offs between levels of local adaptation that can be achieved in the two habitats.

Convergence stability

A singular strategy p^* is convergence stable, and thus attainable trough gradual evolution, if the derivative of the selection gradient evaluated at the singular strategy is negative (Geritz et al. 1997),

$$\left(\frac{\partial D_p(p,h)}{\partial p} \right)_{p=p^*} < 0 . \qquad \text{(B5)}$$

For Model 1, we obtain

$$c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)} < c_1 \frac{w_1'(p^*)^2}{w_1(p^*)^2} + c_2 \frac{w_2'(p^*)^2}{w_2(p^*)^2} . \qquad \text{(B6)}$$

For Model 2, we obtain

$$(1-h)w_1''(p^*) + hw_2''(p^*) < 0 . \qquad \text{(B7)}$$

For Model 3, we obtain

$$c_1 w_1''(p^*) + c_2 w_2''(p^*) < 0 . \qquad \text{(B8)}$$

Local evolutionary stability

A singular strategy is locally evolutionary stable, and thus immune against invasion by neighboring strategies, if it locally maximizes invasion fitness relatively to variant traits. The second derivative of invasion fitness taken with respect to the variant strategy and evaluated at the singular strategy must then be negative,

$$\left(\frac{\partial^2 s_{p,h}(\tilde{p},h)}{\partial \tilde{p}^2} \right)_{\tilde{p}=p=p^*} < 0 . \qquad \text{(B9)}$$

For Model 1, we obtain

$$c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)} < 0 . \tag{B10}$$

For Model 2, we obtain

$$(1-h) w_1''(p^*) + h w_2''(p^*) < 0 . \tag{B11}$$

For Model 3, we obtain

$$c_1 w_1''(p^*) + c_2 w_2''(p^*) < 0 . \tag{B12}$$

Global evolutionary stability of protected dimorphisms

Even when a protected dimorphism cannot emerge through gradual evolution, it may appear through mutations or recombinations of particularly large phenotypic effect, or through the immigration of non-resident strategies from the outside. Such a dimorphism is globally evolutionarily stable, and thus immune against the invasion of intermediate strategies, if the invasion fitnesses of all intermediate strategies are negative in the population of the two resident strategies. For Model 1 with fixed random dispersal ($h = c_2$), the invasion fitness of a variant strategy $\tilde{p}$ in a dimorphic population with the resident specialist strategies $p_1 = 0$ and $p_2 = 1$ is then given by

$$s_{0,1}(\tilde{p}) = \ln \frac{w_1(\tilde{p})[w_2(1) - w_2(0)] + w_2(\tilde{p})[w_1(0) - w_1(1)]}{w_1(0) w_2(1) - w_1(1) w_2(0)} . \tag{B13}$$

With $w_1(0) = w_2(1) = 1$ and $w_1(1) = w_2(0) = 1 - s$, this gives

$$s_{0,1}(\tilde{p}) = \ln \frac{w_1(\tilde{p}) + w_2(\tilde{p})}{2 - s} . \tag{B14}$$

This invasion fitness assumes positive values if and only if the trade-off is weak. Hence, the considered dimorphism is globally evolutionarily stable if and only if the trade-off is strong. If we assume matching habitat choice ($h_1 = 0$ and $h_2 = 1$) instead of fixed random dispersal, the invasion fitness of local-adaptation trait $\tilde{p}$ with a habitat-choice trait $\tilde{h}$ in a dimorphism of specialists is given by

$$s_{0,1}(\tilde{p}) = \ln((1-\tilde{h})w_1(\tilde{p}) + \tilde{h}w_2(\tilde{p})) . \tag{B15}$$

This invasion fitness can never assume positive values, and hence the considered dimorphism is always globally evolutionarily stable.

C – Evolution of habitat choice alone

Selection gradients and singular strategies

As before, the selection gradient is defined as the derivative of invasion fitness taken with respect to the variant strategy and evaluated at the resident strategy,

$$D_h(p,h) = \left(\frac{\partial s_{p,h}(p,\tilde{h})}{\partial \tilde{h}} \right)_{\tilde{h}=h} . \tag{C1}$$

For Model 1, we obtain

$$D_h(p,h) = \frac{c_2}{h} - \frac{c_1}{1-h} \tag{C2}$$

and thus the singular habitat-choice trait

$$h^* = c_2 . \tag{C3}$$

For Model 2, we obtain

$$D_h(p,h) = \frac{w_2(p) - w_1(p)}{(1-h)w_1(p) + hw_2(p)} . \tag{C4}$$

Since the numerator of this expression does not vanish unless local fitness is the same in both habitats, selection on habitat choice in Model 2 typically stays directional, favoring maximal preference to the habitat in which local fitness is highest. For Model 3, we obtain

$$D_h(p,h) = \frac{(1-h)c_2 w_2(p) - hc_1 w_1(p)}{(1-h)h[c_1 w_1(p) + c_2 w_2(p)]} \tag{C5}$$

and thus the singular habitat-choice trait

$$h^* = \frac{c_1 w_1(p)}{c_1 w_1(p) + c_2 w_2(p)}. \tag{C6}$$

Convergence stability

For Model 1, the singular habitat-choice trait is convergence stable if

$$c_1^{-1} + c_2^{-1} > 0, \tag{C7}$$

which is always true. For Model 3, the singular habitat-choice trait is convergence stable if

$$\frac{[c_1 w_1(p) + c_2 w_2(p)]^2}{c_1 c_2 w_1(p) w_2(p)} > 0, \tag{C8}$$

which again is always true. Hence, in both models the singular habitat-choice trait is always convergence stable.

Local evolutionary stability

For Models 1 and 3, we obtain

$$\left(\frac{\partial^2 s_{p,h}(p,\tilde{h})}{\partial \tilde{h}^2} \right)_{\tilde{h}=h=h^*} = 0. \tag{C9}$$

For Models 1 and 3, rare habitat-choice variants in the neighborhood of the singular habitat-choice trait are thus always selectively neutral. Therefore, when the singular habitat-choice trait is convergence stable, the population will evolve to it and stay in its neighborhood. This is what we refer to as neutrally ES.

D – Joint evolution of local adaptation and habitat choice

We now consider the joint evolution of habitat choice and local adaptation using methods presented by Meszéna et al. (2001) and Leimar (2005, in press). A strategy is then always described by a vector (p,h) of two trait values.

Selection gradients and singular strategies

The selection gradient for joint evolution is the vector $(D_p(p,h), D_h(p,h))$ of the two partial derivatives of the invasion fitness taken with respect to the two variant traits and evaluated at the resident strategy. For Model 1, we obtain

$$\begin{cases} D_p(p,h) = c_1 \dfrac{w_1'(p)}{w_1(p)} + c_2 \dfrac{w_2'(p)}{w_2(p)} \\ D_h(p,h) = \dfrac{c_2}{h} - \dfrac{c_1}{1-h} \end{cases}, \tag{D1}$$

and the singular strategy (p^*, h^*) is thus given by

$$\begin{cases} c_1 \dfrac{w_1'(p^*)}{w_1(p^*)} + c_2 \dfrac{w_2'(p^*)}{w_2(p^*)} = 0 \\ h^* = c_2 \end{cases}. \tag{D2}$$

For Model 2, we obtain

$$\begin{cases} D_p(p,h) = \dfrac{(1-h)w_1'(p) + hw_2'(p)}{(1-h)w_1(p) + hw_2(p)} \\ D_h(p,h) = \dfrac{w_2(p) - w_1(p)}{(1-h)w_1(p) + hw_2(p)} \end{cases}, \tag{D3}$$

and

$$\begin{cases} w_1(p^*) = w_2(p^*) \\ h^* = \dfrac{w_1'(p^*)}{w_1'(p^*) - w_2'(p^*)} \end{cases}. \tag{D4}$$

For Model 3, we obtain

$$\begin{cases} D_p(p,h) = \dfrac{c_1 w_1'(p) + c_2 w_2'(p)}{c_1 w_1(p) + c_2 w_2(p)} \\ D_h(p,h) = \dfrac{(1-h)c_2 w_2(p) - hc_1 w_1(p)}{(1-h)h[c_1 w_1(p) + c_2 w_2(p)]} \end{cases}, \tag{D5}$$

and

$$\begin{cases} c_1 w_1'(p^*) + c_2 w_2'(p^*) = 0 \\ h^* = \dfrac{c_1 w_1(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)} \end{cases} . \tag{D6}$$

Convergence stability

A two-trait singular strategy (p^*, h^*) is convergence stable if the Jacobian matrix $\tilde{J}$ of the evolutionary dynamics possesses only eigenvalues with negative real parts. This is the case if and only if the determinant of $\tilde{J}$ (which equals the product of $\tilde{J}$'s two eigenvalues) is positive and its trace (which equals the sum of $\tilde{J}$'s two eigenvalues) is negative. $\tilde{J}$ can be computed as the product of two matrices, $\tilde{J} = JV$: the Jacobian matrix J of the selection gradient,

$$J = \begin{pmatrix} \dfrac{\partial D_p(p,h)}{\partial p} & \dfrac{\partial D_p(p,h)}{\partial h} \\ \dfrac{\partial D_h(p,h)}{\partial p} & \dfrac{\partial D_h(p,h)}{\partial h} \end{pmatrix}_{p=p^*,\, h=h^*} , \tag{D7}$$

and the (population-level or mutational) variance-covariance matrix V ,

$$V = \begin{pmatrix} V_{pp} & V_{ph} \\ V_{ph} & V_{hh} \end{pmatrix} . \tag{D8}$$

Excluding biologically degenerate cases, trait variances are always positive, $V_{pp}, V_{hh} > 0$, and their product always exceeds the squared covariance, $V_{pp} V_{hh} > V_{ph}^2$.

For Model 1, we obtain

$$J = \begin{pmatrix} c_1 \dfrac{w_1''(p^*)}{w_1(p^*)} + c_2 \dfrac{w_2''(p^*)}{w_2(p^*)} - c_1 \dfrac{w_1'(p^*)^2}{w_1(p^*)^2} - c_2 \dfrac{w_2'(p^*)^2}{w_2(p^*)^2} & 0 \\ 0 & -(c_1^{-1} + c_2^{-1}) \end{pmatrix} \tag{D9}$$

and thus

$$\det JV = -(V_{pp} V_{hh} - V_{ph}^2)(c_1^{-1} + c_2^{-1}) \left(c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)} - c_1 \frac{w_1'(p^*)^2}{w_1(p^*)^2} - c_2 \frac{w_2'(p^*)^2}{w_2(p^*)^2} \right) \tag{D10}$$

together with

$$\operatorname{tr} JV = V_{pp}\left(c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)} - c_1 \frac{w_1'(p^*)^2}{w_1(p^*)^2} - c_2 \frac{w_2'(p^*)^2}{w_2(p^*)^2} \right) - V_{hh}(c_1^{-1} + c_2^{-1})\,. \tag{D11}$$

Both eigenvalues of JV have negative real parts if and only if their product is positive ($\det JV > 0$) and their sum is negative ($\operatorname{tr} JV < 0$), which applies if and only if

$$c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)} < c_1 \frac{w_1'(p^*)^2}{w_1(p^*)^2} + c_2 \frac{w_2'(p^*)^2}{w_2(p^*)^2}\,. \tag{D12}$$

Hence, the singular strategy (p^*, h^*) is convergence stable, independent of trait variances and covariance, if and only if equation (D12) is fulfilled, i.e., for weak and moderately strong trade-offs. It is worth highlighting that this is the same condition that describes convergence stability when local adaptation evolves alone (eq. [3c]). For very strong trade-offs, equation (D12) is not fulfilled and $\det JV < 0$. This implies that the eigenvalues of JV are real with opposite signs, so that the singular strategy (p^*, h^*) then is an evolutionary saddle point, independent of the variance-covariance matrix.

For Model 2, we obtain

$$J = \begin{pmatrix} (1-h)w_1''(p^*) + hw_2''(p^*) & w_2'(p^*) - w_1'(p^*) \\ w_2'(p^*) - w_1'(p^*) & 0 \end{pmatrix} \tag{D13}$$

and thus

$$\det JV = -\frac{(V_{pp}V_{hh} - V_{ph}^2)[w_1'(p^*) - w_2'(p^*)]^2}{[(1-h^*)w_1(p^*) + h^* w_2(p^*)]^2}\,, \tag{D14}$$

which is always negative. Accordingly, the eigenvalues of JV are real with opposite signs, so that the singular strategy (p^*, h^*) lacks convergence stability and is an evolutionary saddle point, independent of the trade-off shape and the variance-covariance matrix.

For Model 3, we obtain

$$J = \begin{pmatrix} \dfrac{c_1 w_1''(p^*) + c_2 w_2''(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)} & 0 \\ \dfrac{w_2'(p^*)}{w_2(p^*)} - \dfrac{w_1'(p^*)}{w_1(p^*)} & -\dfrac{[c_1 w_1(p^*) + c_2 w_2(p^*)]^2}{c_1 c_2 w_1(p^*) w_2(p^*)} \end{pmatrix} \tag{D15}$$

and thus

$$\det JV = -\frac{(V_{pp} V_{hh} - V_{ph}^2)[c_1 w_1(p^*) + c_2 w_2(p^*)][c_1 w_1''(p^*) + c_2 w_2''(p^*)]}{c_1 c_2 w_1(p^*) w_2(p^*)} \tag{D16}$$

together with

$$\operatorname{tr} JV = V_{pp} \frac{c_1 w_1''(p^*) + c_2 w_2''(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)} - V_{hh} \frac{[c_1 w_1(p^*) + c_2 w_2(p^*)]^2}{c_1 c_2 w_1(p^*) w_2(p^*)} + V_{ph} \left(\frac{w_2'(p^*)}{w_2(p^*)} - \frac{w_1'(p^*)}{w_1(p^*)} \right). \tag{D17}$$

The condition $\det JV > 0$ thus applies if and only if

$$c_1 w_1''(p^*) + c_2 w_2''(p^*) < 0, \tag{D18}$$

while the condition $\operatorname{tr} JV < 0$ applies if and only if

$$\frac{c_1 w_1''(p^*) + c_2 w_2''(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)} < \frac{V_{hh}}{V_{pp}} \frac{[c_1 w_1(p^*) + c_2 w_2(p^*)]^2}{c_1 c_2 w_1(p^*) w_2(p^*)} - \frac{V_{ph}}{V_{pp}} \left(\frac{w_2'(p^*)}{w_2(p^*)} - \frac{w_1'(p^*)}{w_1(p^*)} \right). \tag{D19}$$

We now have to distinguish three cases, according to the sign and magnitude of the left-hand side of equation (D19). First, when the trade-off is strong (i.e., eq. [D18] is not fulfilled), $\det JV < 0$, so the eigenvalues of JV are real with opposite signs and the singular strategy (p^*, h^*) is an evolutionary saddle point, independent of the variance-covariance matrix. Second, when the trade-off is very weak, i.e.,

$$\frac{c_1 w_1''(p^*) + c_2 w_2''(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)} < -\frac{1}{4} \frac{c_1 c_2 w_1(p^*) w_2(p^*)}{[c_1 w_1(p^*) + c_2 w_2(p^*)]^2} \left(\frac{w_2'(p^*)}{w_2(p^*)} - \frac{w_1'(p^*)}{w_1(p^*)} \right)^2, \tag{D20}$$

$\operatorname{tr} JV < 0$ applies independent of the variance-covariance matrix. To see this, notice that the right-hand side of equation (D20) is the minimum m that the right-hand side of equation (D19) can assume upon variation of $v_{hh} = V_{hh} / V_{pp}$ and $v_{ph} = V_{ph} / V_{pp}$ subject to the consistency condition $v_{hh} > v_{ph}^2$: $m = -\tfrac{1}{4} x_{hh}^{-1} x_{ph}^2$ at $v_{ph} = \sqrt{v_{hh}}$ and $v_{hh} = \tfrac{1}{2} x_{hh}^{-2} x_{ph}^2$, where

$x_{hh} > 0$ and $x_{ph} > 0$ are, respectively, the coefficients of v_{hh} and v_{ph} on the right-hand side $v_{hh}x_{hh} + v_{ph}x_{ph}$ of equation (D19). Since equation (D20) thus ensures $\det JV > 0$ and $\operatorname{tr} JV < 0$, both eigenvalues of JV have negative real parts and the singular strategy (p^*, h^*) is convergence stable independent of the variance-covariance matrix. Third, when the trade-off is moderately weak, equation (D18) is fulfilled, so $\det JV > 0$, but equation (D20) is not fulfilled, so the sign of $\operatorname{tr} JV$ depends on the variance-covariance matrix according to equation (D17). Therefore, convergence stability depends on the variance-covariance matrix: the singular strategy (p^*, h^*) then is convergence stable unless the covariance between the local-adaptation trait and the habitat-choice trait is positive and larger than a threshold that rises for trade-offs that are increasingly weak,

$$V_{ph} > \frac{V_{hh} \dfrac{[c_1 w_1(p^*) + c_2 w_2(p^*)]^2}{c_1 c_2 w_1(p^*) w_2(p^*)} - V_{pp} \dfrac{c_1 w_1''(p^*) + c_2 w_2''(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)}}{\dfrac{w_2'(p^*)}{w_2(p^*)} - \dfrac{w_1'(p^*)}{w_1(p^*)}}. \tag{D21}$$

If the trade-off is weak and equation (D21) is fulfilled, the singular strategy (p^*, h^*) is a repellor (Appendix fig. 1).

Local evolutionary stability

A two-trait singular strategy (p^*, h^*) is locally evolutionarily stable if the Hessian matrix

$$H = \begin{pmatrix} \dfrac{\partial^2 s_{p,h}(\tilde{p},\tilde{h})}{\partial \tilde{p}^2} & \dfrac{\partial^2 s_{p,h}(\tilde{p},\tilde{h})}{\partial \tilde{p} \partial \tilde{h}} \\ \dfrac{\partial^2 s_{p,h}(\tilde{p},\tilde{h})}{\partial \tilde{p} \partial \tilde{h}} & \dfrac{\partial^2 s_{p,h}(\tilde{p},\tilde{h})}{\partial \tilde{h}^2} \end{pmatrix}_{\tilde{p}=p=p^*,\, \tilde{h}=h=h^*} \tag{D22}$$

is negative definite. Notice that, in contrast to J above, the matrix H is always symmetric. Since the two-trait singular strategy is never convergence stable for Model 2, below we only consider its evolutionary stability for Models 1 and 3. For Model 1, we obtain

$$H = \begin{pmatrix} c_1 \dfrac{w_1''(p^*)}{w_1(p^*)} + c_2 \dfrac{w_2''(p^*)}{w_2(p^*)} & \dfrac{w_2'(p^*)}{w_2(p^*)} - \dfrac{w_1'(p^*)}{w_1(p^*)} \\ \dfrac{w_2'(p^*)}{w_2(p^*)} - \dfrac{w_1'(p^*)}{w_1(p^*)} & 0 \end{pmatrix}. \tag{D23}$$

For Model 3, we obtain

$$H = \begin{pmatrix} \dfrac{c_1 w_1''(p^*) + c_2 w_2''(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)} & \dfrac{w_2'(p^*)}{w_2(p^*)} - \dfrac{w_1'(p^*)}{w_1(p^*)} \\ \dfrac{w_2'(p^*)}{w_2(p^*)} - \dfrac{w_1'(p^*)}{w_1(p^*)} & 0 \end{pmatrix}. \tag{D24}$$

Both matrixes above possess a negative determinant; hence, they are not negative definite and the singular strategy is a saddle point of the fitness landscape, that is, ES in some directions and not ES in other directions.

Mutual invasibility

The direction in which a dimorphism of strategies diverges from an evolutionary branching point is given by $v = Vg$, where V is the variance-covariance matrix and g is the dominant eigenvector of the Hessian matrix H. Mutual invasibility applies when each strategy in this dimorphism can invade the other, causing the dimorphism to be protected. This is ensured if and only if $v^{\mathrm{T}}Mv$ is positive, where $M = H - J_{\mathrm{s}}$ is the difference between the Hessian matrix H and the symmetrised Jacobian matrix J_{s}. For Model 1, we obtain

$$v^{\mathrm{T}}Mv = z(XV_{pp} + V_{ph})^2 + 2y(XV_{pp} + V_{ph})(V_{hh} + XV_{ph}) + c_1^{-1}c_2^{-1}(V_{hh} + XV_{ph})^2, \tag{D25}$$

where

$$x = c_1 \frac{w_1''(p^*)}{w_1(p^*)} + c_2 \frac{w_2''(p^*)}{w_2(p^*)}, \tag{D26}$$

$$y = \frac{w_2'(p^*)}{w_2(p^*)} - \frac{w_1'(p^*)}{w_1(p^*)}, \tag{D27}$$

$$z = c_1 \frac{w_1'(p^*)^2}{w_1(p^*)^2} + c_2 \frac{w_2'(p^*)^2}{w_2(p^*)^2}, \tag{D28}$$

and

$$X = \frac{x + \sqrt{x^2 + 4y^2}}{2y}. \tag{D29}$$

In equation (D25), all terms are positive or zero, except V_{ph}, which can be negative. Hence, in the absence of covariance between the two traits ($V_{ph} = 0$), or when the traits are positively correlated ($V_{ph} > 0$), $v^{\mathrm{T}}Mv$ is always positive, ensuring that dimorphisms emerging around the evolutionary branching point are protected. The genetic covariance between the local-adaptation trait and the habitat-choice trait may obstruct the emergence of such dimorphisms only when it is sufficiently negative, falling below a threshold that depends on the shape of the trade-off, the relative habitat frequencies, and the genetic variances of the two traits,

$$V_{ph} < -\frac{X(Xy+z)V_{pp} + (c_1^{-1}c_2^{-1}X + y)V_{hh} + \sqrt{(X^2V_{pp} - V_{hh})^2(y^2 - c_1^{-1}c_2^{-1}z)}}{c_1^{-1}c_2^{-1}X^2 + 2Xy + z}. \tag{D30}$$

For Model 3, we obtain

$$v^{\mathrm{T}}Mv = (V_{hh} + XV_{ph})[(XV_{pp} + V_{ph})y + (V_{hh} + XV_{ph})z], \tag{D31}$$

where

$$x = \frac{c_1 w_1''(p^*) + c_2 w_2''(p^*)}{c_1 w_1(p^*) + c_2 w_2(p^*)}, \tag{D32}$$

$$y = \frac{w_2'(p^*)}{w_2(p^*)} - \frac{w_1'(p^*)}{w_1(p^*)}, \tag{D33}$$

$$z = \frac{[c_1 w_1(p^*) + c_2 w_2(p^*)]^2}{c_1 c_2 w_1(p^*) w_2(p^*)}, \tag{D34}$$

and

$$X = \frac{x + \sqrt{x^2 + 4y^2}}{2y}. \tag{D35}$$

In equation (D31), all terms are positive or zero, except V_{ph}, which can be negative. Hence, in the absence of covariance between the two traits ($V_{ph} = 0$), or when the traits are positively correlated ($V_{ph} > 0$), $v^{\mathrm{T}} M v$ is always positive, ensuring that dimorphisms emerging around the evolutionary branching point are protected. The genetic covariance between the local-adaptation trait and the habitat-choice trait may obstruct the emergence of such dimorphisms only when it is sufficiently negative, falling below a threshold that depends on the shape of the trade-off, the relative habitat frequencies, and the genetic variances of the two traits,

$$V_{ph} < \max\left(-\frac{V_{hh}}{X}, -\frac{XyV_{pp} - zV_{hh}}{Xz + y} \right). \tag{D36}$$

E – Invasion boundaries

The invasion boundary of a resident strategy is defined as the set of strategies, unconstrained by a trade-off, that have the same fitness as the resident strategy (de Mazancourt and Dieckmann 2004; Rueffler et al. 2004). Their analysis enables understanding the evolutionary implications of trade-offs (fig. 4).

Evolution of local adaptation alone

For fixed and monomorphic habitat choice h, the invasion boundary of a resident strategy $(w_1(p), w_2(p))$ is given by the set of local fitnesses $(\hat{w}_1, \hat{w}_2)$ that imply vanishing invasion fitness. For Model 1, we obtain

$$\ln\left(c_1 \frac{\hat{w}_1}{w_1(p)} + c_2 \frac{\hat{w}_2}{w_2(p)} \right) = 0, \tag{E1}$$

which yields

$$\hat{w}_2 = \frac{w_2(p)}{c_2} - \frac{c_1 w_2(p)}{c_2 w_1(p)} \hat{w}_1. \tag{E2}$$

For Model 2, we obtain

$$\hat{w}_2 = \frac{1-h}{h} w_1(p) + w_2(p) - \frac{1-h}{h} \hat{w}_1 . \tag{E3}$$

For Model 3, we obtain

$$\hat{w}_2 = \frac{c_1}{c_2} w_1(p) + w_2(p) - \frac{c_1}{c_2} \hat{w}_1 . \tag{E4}$$

In all three models, the invasion boundary $\hat{w}_2(\hat{w}_1)$ is therefore linear.

Joint evolution of local adaptation and habitat choice

Under joint evolution, the invasion boundary of a resident strategy $(w_1(p), w_2(p), h)$ is given by the set of strategies $(\hat{w}_1, \hat{w}_2, \hat{h})$ that imply vanishing invasion fitness. For Model 1, we obtain

$$\hat{w}_2 = \frac{h w_2(p)}{c_2 \hat{h}} - \frac{c_1 h (1-\hat{h}) w_2(p)}{c_2 \hat{h} (1-h) w_1(p)} \hat{w}_1 . \tag{E5}$$

For Model 2, we obtain

$$\hat{w}_2 = \frac{1-h}{\hat{h}} w_1(p) + \frac{h}{\hat{h}} w_2(p) - \frac{1-\hat{h}}{\hat{h}} \hat{w}_1 . \tag{E6}$$

For Model 3, we obtain

$$\hat{w}_2 = \frac{c_1 h}{c_2 \hat{h}} w_1(p) + \frac{h}{\hat{h}} w_2(p) - \frac{c_1 h (1-\hat{h})}{c_2 \hat{h} (1-h)} \hat{w}_1 . \tag{E7}$$

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Table 1

OVERVIEW OF SOME MODELS ADDRESSING THE EVOLUTION AND COEXISTENCE OF SPECIALISTS AND GENERALISTS IN HETEROGENEOUS ENVIRONMENTS

Reference	Focal research question	Regulation and habitat output	Local-adaptation trade-off	Habitat-choice evolution	Habitat-choice mechanism
Abrams 2006b	1	3	5	1	3, 4
Balkau and Feldman 1973	1	1	1	1	2
Beltman and Haccou 2005	2	3	5	2	4
Beltman et al. 2004	1	3	5	1	4
Beltman and Metz 2005	2	3	5	2	4, 5
Brown 1990	2	3	3	1, 2	4, 5
Brown 1998	2	3	3	1, 2	4, 5
Brown and Pavlovic 1992	2	3	6	1	2
Bulmer 1972	1	1	1	1	2
Castillo-Chavez et al. 1988	1	2	2	2	5
Christiansen 1974	1	1	1	1	2
Christiansen 1975	1	1, 3	1	1	2
Czochor and Leonard 1982	1	1, 2	1	1	1
Day 2001	2	3	5	1	2
de Meeûs and Goudet 2000	2	1, 2	2	1	1
de Meeûs et al. 1993	1, 2	1, 2	1	1, 2	1, 3
Deakin 1966	1	1	1	1	2
Deakin 1968, 1972	1	1	1	1	2
Dempster 1955	1	2	1	1	1

Diehl and Bush 1989	1	1	1	2	2, 5
Doyle 1975	4	1, 2	1	2	5
Egas et al. 2004	1, 2	3	5	1	3
Fretwell and Lucas 1970; Fretwell 1972	4	1, 3	1	2	3
Fry 2003	2	1	4	2	5
Fryxell 1997	4	3	1	2	5
Garcia-Dorado 1986	1	1	1	1	3
Garcia-Dorado 1987	1	1	1	2	3
Gliddon and Strobeck 1975	1	1	1	1	1
Hedrick 1990a	1	1	1	1	3
Hedrick 1990b	1	1, 3	1	1	3
Holsinger and Pacala 1990	2	1, 2	1	1	1
Holt and Gaines 1992	2	2	2	1	2
Holt 1985	4	1, 3	1	2	3
Jaenike and Holt 1991	2	2, 3	1	1	3, 5
Johnson et al. 1996	1	1	1	2	2, 5
Karlin and McGregor 1972	1	1	1	1	2
Karlin and Campbell 1981	1	1, 2	1	1	1,2
Karlin 1982	1	1, 2	1	1	1,2
Kawecki 1997	1	1	6	2	2, 5
Kisdi and Geritz 1999	2	1	5	1	2
Kisdi 2001	2	1	6	1	1
Kisdi 2002	2	3	5	2	2

Lawlor and Maynard Smith 1976	1	3	6	1, 2	5
Levene 1953	1	1	1	1	1
Levins 1962	1	2, 3	6	1	1
Levins 1963	1	1, 2	5	1	4, 5
Levins and McArthur 1966	1	1	5	1	1, 2
MacArthur and Levins 1964	1	2	1	1	1, 2
MacArthur and Levins 1967	1	1	5	1	5
Maynard Smith 1966	1	1	1	1	2
Maynard Smith and Hoekstra 1980	1	1	1	1	2
McPeek and Holt 1992	4	1	1	2	2, 4
Meszéna et al. 1997	2	1	5	1	2
Muko and Iwasa 1999	1	1,3	1	1	1
Nurmi and Parvinen 2008	2	3	5	1	2
Prout 1968	1	1	1	1	1, 2
Rausher 1984	1, 4	1	1	2	5
Rausher and Englander 1987	1, 4	1	1	2	5
Ravigné et al. 2004	1	1, 2, 3	1	1	1, 3
Robinson and Wilson 1998	1	3	5	1	3
Rosenzweig 1981	1	3	6	2	4, 5
Rueffler et al. 2006b	2	1, 3	5	1	1
Rueffler et al. 2007	2	1, 3	5	2	3, 4
Sasaki and de Jong 1999	2	1, 2, 3	5	1	2

Spichtig and Kawecki 2004	1	1	5	1	2
Templeton and Rothman 1981	1	1, 2	1	1	3
van Tienderen 1991	3	1, 2	5	1	1
van Tienderen 1997	3	1, 2	5	1	1
Ward 1987	4	1, 2	1	2	5
Wiener and Feldman 1993	1	1	1	1	2
Wilson and Yoshimura 1994	1	1, 3	5	1	3
Yukilevich and True 2006	1	1	1	1	2
Present study	1, 2, 4	1, 2, 3	6	1, 2	5

Note. - While most of the 72 models listed in the table adopt a focus on the population ecology and evolutionary ecology of specialization, a few representative models based on community ecology have also been included. The classification below is based on five characteristic dimensions of model differentiation. Focal research question: 1 = Maintenance of a local-adaptation polymorphism; 2 = Emergence of a local-adaptation polymorphism; 3 = Quantitative genetics of local adaptation; 4 = Habitat-choice evolution under fixed local adaptation. Regulation and habitat output: 1 = Local regulation and constant (trait-independent) habitat output (Model 1); 2 = Global regulation (Model 2); 3 = Local regulation and variable (trait-dependent) habitat output (Model 3). Local-adaptation trade-off: 1 = Does not matter; 2 = Linear; 3 = Weak; 4 = Strong; 5 = Particular trade-off function; 6 = General trade-off function. Habitat-choice evolution: 1 = No; 2 = Yes. Host-choice mechanism: 1 = No habitat choice (random dispersal). 2 = Philopatry; 3 = Matching habitat choice (pleiotropically determined by local adaptation); 4 = Learned or plastic habitat choice; 5 = Habitat choice based on a two-allele mechanism (independent of local adaptation).

Figure captions

Figure 1. Evolutionary outcomes predicted for simple analytical two-deme dispersal-selection models in dependence on the sequence of life-cycle events, on the shape of the local-adaptation trade-off, and on whether or not habitat choice and local adaptation evolve jointly. Shaded area: conditions under which habitat-choice evolution qualitatively changes local-adaptation evolution. Hatched area: conditions under which local-adaptation evolution qualitatively changes habitat-choice evolution. For Model 3 with moderately weak trade-offs, the population-level or mutational covariance between the local-adaptation trait and the habitat-choice trait is assumed not to be too strongly positive. All other results are valid in general, irrespective of the variance-covariance structure of the two traits.

Figure 2. Evolutionarily singular local-adaptation strategies resulting for different trade-off strengths. Dotted curves: the singular strategy is an evolutionary repellor (not CS). Selection is divergent and favors the emergence of a single specialist. Dashed curves: the singular strategy is an evolutionary branching point (CS but not ES). Selection is disruptive and favors the emergence of two coexisting specialists. Thick continuous curves: the singular strategy is an evolutionary attractor (both CS and ES). Selection is stabilizing and favors intermediate levels of adaptation, tuned by habitat choice in Model 2 and by habitat carrying capacities in Models 1 and 3. Arrows indicate the direction of selection. A) Constant (trait-independent) and symmetric habitat outputs (Model 1 with $c_1 = c_2$). Selection favors generalists for weak trade-offs, two coexisting specialists for moderately strong trade-offs, and a single specialist for very strong trade-offs. B) Constant and asymmetric habitat outputs (Model 1 with $c_1 = 0.4$ and $c_2 = 0.6$). The range of moderately strong trade-offs that cause the emergence of two coexisting specialists is narrowed compared to the symmetric case. C) Variable (trait-dependent) and symmetric habitat outputs (Model 2 with $h = 0.5$, or equivalently, Model 3

with $c_1 = c_2$). No evolutionary branching can occur. Selection favors either a generalist (for weak trade-offs) or a single specialist (for strong trade-offs). D) Variable and asymmetric habitat outputs (Model 2 with $h = 0.6$, or equivalently, Model 3 with $c_1 = 0.4$ and $c_2 = 0.6$). Specialization is now biased toward the most frequent (or productive) habitat. Other parameter: $s = 0.8$.

Figure 3. Joint evolutionary dynamics of local adaptation and habitat choice. Gray arrows depict the direction of the selection gradient, which determines selection pressures on both traits. Thick curves with black arrows show evolutionary trajectories for equal trait variances and absent trait covariance. Black circles represent alternative end points of the evolutionary process. Grey circles represent evolutionary branching points. Open circles represent evolutionary repellors. Dotted lines separate the basins of attraction of two alternative evolutionary end points; these lines are known as separatrices. A-C) For very strong trade-offs, all three life cycles give rise to evolutionary bistability between two alternative evolutionary outcomes (here illustrated for $\gamma = 0.2$). Under local regulation (Models 1 and 3), the initial local-adaptation trait determines whether the population specializes on one habitat or the other, whereas the initial habitat-choice trait has no effect on the evolutionary outcome (A and B). In contrast, under global regulation (Model 2), the initial habitat-choice trait affects the evolutionary outcome together with the initial habitat-choice trait (C). D) For weak and moderately strong trade-offs, life cycles with local regulation and constant habitat outputs (Model 1) may select for the emergence of two coexisting specialists through gradual evolution (here illustrated for $\gamma = 0.9$). E) For weak trade-offs, life cycles with local regulation and variable habitat outputs (Model 3) may select for the emergence of two coexisting specialists (here illustrated for $\gamma = 1.2$). In both D and E, the joint evolution of local adaptation and habitat choice first converges to the evolutionary branching point, before

splitting into two increasingly specialized morphs as indicated by the double-headed dashed arrows. F) Under global regulation (Model 2), the angle of the separatrix between the basins of attraction of the two specialists varies with the trade-off strength γ. For weaker trade-offs (larger γ), the separatrix is less steep, which implies that the initial habitat-choice trait has a greater influence on the evolutionary outcome than the initial local-adaptation trait. For stronger trade-offs (smaller γ), the separatrix is steeper, which implies that that the relative importance of initial trait values is reversed. All panels are representative also of evolutionary dynamics with some covariance between local-adaptation and habitat-choice traits, unless the covariance is strongly positive in Model 3 or strongly negative in Models 1 and 3. Other parameters: $s = 0.8$, $c_1 = 0.4$, and $c_2 = 0.6$.

Figure 4. Geometrical interpretation of why habitat-choice evolution qualitatively changes local-adaptation evolution under weak trade-offs. All illustrations focus on Model 1 with genetically independent traits (absent covariance) of equal variance. A) This panel shows a weak local-adaptation trade-off (thick line, for $s = 0.9$ and $\gamma = 1.2$), the singular resident at $p = 0.5$ (open circle), and its invasion boundary (thin line). Habitat choice is fixed at $h = 0.5$. Only variants above the invasion boundary (white region) can invade the corresponding resident, while those below (gray region) cannot. The resident thus is evolutionarily stable, as no variant constrained by the trade-off can invade it. B) The local-adaptation trade-off is now strong ($s = 0.9$ and $\gamma = 0.7$). The singular resident at $p = 0.5$ (open circle) can be invaded by any variant lying above the invasion boundary (white region). Since this includes variants permitted by the trade-off, the resident is not evolutionarily stable. C-D) Extension of preceding considerations to the joint evolution of local adaptation and habitat choice. Three-dimensional trade-off (light gray surface) and invasion boundary (dark gray surface) of the singular resident $(p = 0.5, h = 0.5)$ (open circle). Under a weak trade-off (C), variants with no

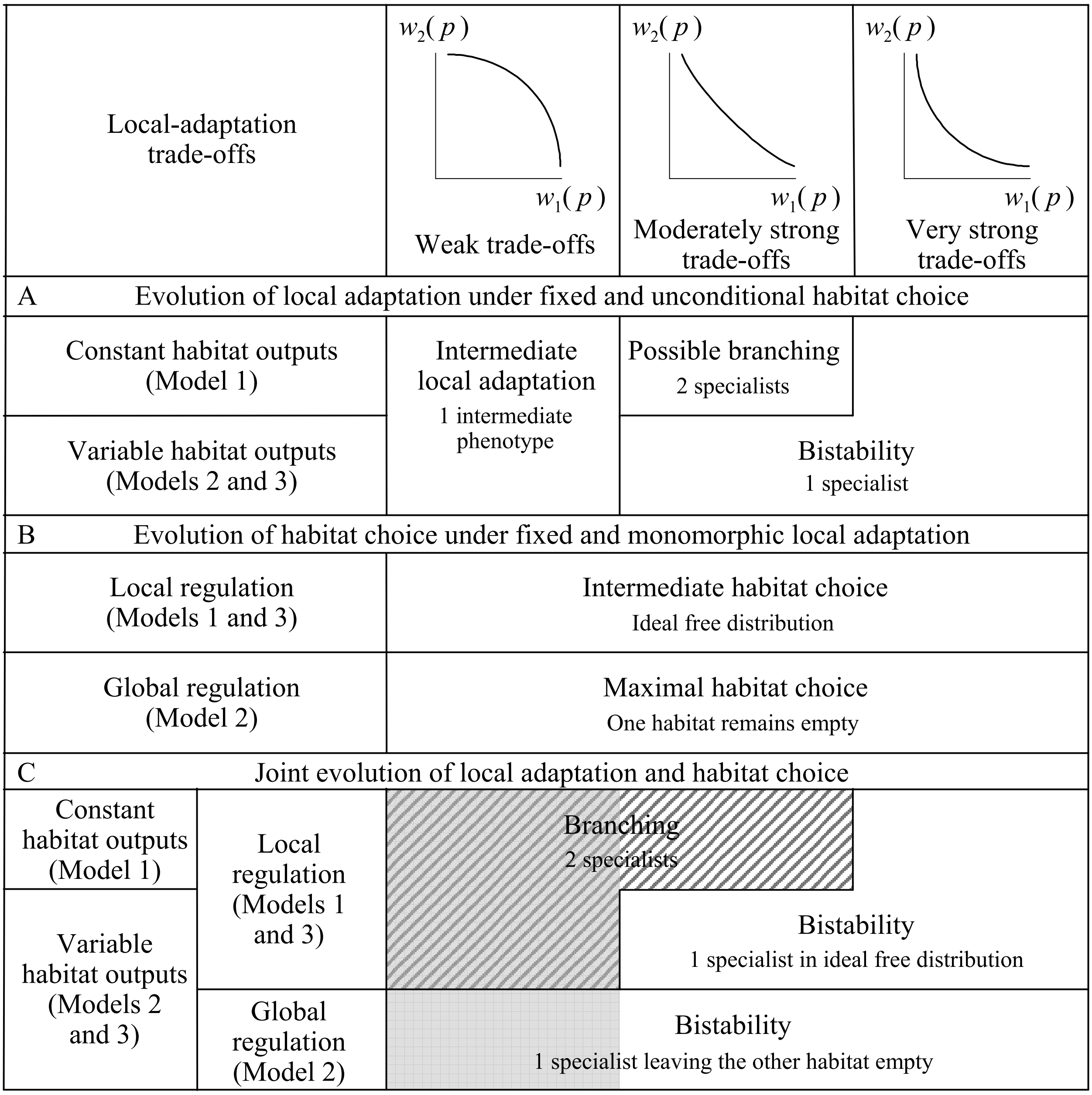
habitat preference (black arrows; $\hat{p} \neq 0.5$ and $\hat{h} = 0.5$) lie below the invasion boundary and therefore cannot invade the resident. When habitat choice is fixed at $h = 0.5$, $p = 0.5$ thus is evolutionarily stable. In contrast, variants whose local-adaption traits and habitat-choice traits differ from the resident in the same direction (white arrows) lie above the invasion boundary and therefore can invade the resident. When habitat choice evolves, $(p = 0.5, h = 0.5)$ thus is not evolutionarily stable. Under a strong trade-off (D), even variants with no habitat preference (black arrows; $\hat{p} \neq 0.5$ and $\hat{h} = 0.5$) can invade the resident. E-F) Fitness landscapes around the singular resident ($p = 0.5$, $h = 0.5$). The darker the gray, the higher the fitness. Dashed lines connect variants $(\hat{p}, \hat{h})$ that experience the same fitness in the resident population. Continuous lines connect variants $(\hat{p}, \hat{h})$ that experience the same fitness as the resident. Under a weak trade-off (E), the resident can only be invaded by variants whose local-adaption traits and habitat-choice traits differ from the resident in the same direction (white arrows). Under a strong trade-off (F), the resident may be invaded also by variants with unchanged habitat-choice traits (black arrows).

Figure 5. Comparison of conditions for the maintenance and emergence of local-adaptation polymorphisms when habitat outputs are constant or variable and habitat choice is fixed and random, fixed and matching, or evolving. The left pair of columns depict conditions for the maintenance of two specialists at $p = 0$ and $p = 1$ (Ravigné et al. 2004) in dependence on the relative carrying capacity c_1 of habitat 1 (horizontal axes) and on the loss s of local fitness that a specialist experiences in the habitat to which it is not adapted (vertical axes), with either fixed and random habitat choice or fixed and matching habitat choice. The right pair of columns depict conditions for the emergence of this polymorphism through gradual evolution

(eqq. [3b] and [3c] for trade-offs of decreasing strength, ranging from $\gamma = 0.2$ (strongest trade-off; black regions) to $\gamma = 1.2$ (weakest trade-off; light gray regions).

Appendix figure 1. Impact of the variance-covariance structure on the joint evolution of local adaptation and habitat choice under local regulation and variable habitat outputs (Model 3). Gray arrows depict the direction of the selection gradient after multiplication with the variance-covariance matrix. Thick curves with black arrows show the resultant evolutionary trajectories. Black circles represent alternative end points of the evolutionary process. The grey circle represents an evolutionary branching point and the open circle an evolutionary repellor. The double-headed dashed arrows depict the direction in which dimorphic strategies diverge from the branching point. The dotted line is the separatrix that separates the basins of attraction of the two alternative evolutionary end points. Habitats occur at equal frequencies ($c_1 = c_2 = 0.5$). The trade-off is moderately weak (i.e., close to linear, $\gamma = 1.1$). The mutational or population-level variance of the local-adaptation trait is $V_{pp} = 4$, while the variance of the habitat-choice trait is $V_{hh} = 1$. A) No covariance between the two traits, $V_{ph} = 0$. The singular strategy is an evolutionary branching point. After convergence to this point, the population splits and becomes dimorphic. B) Maximal positive covariance between the two traits, $V_{ph} = 2$. The singular strategy is an evolutionary repellor. It can never be attained through gradual evolution, and the population instead specializes on one habitat or the other, depending on initial conditions. For some smaller values of V_{ph} (such as $V_{ph} = 1.7$), the evolutionary repellor is surrounded by an evolutionary limit cycle along which the local-adaptation trait and the habitat-choice trait oscillate in perpetuity (result not shown; Red Queen evolution *sensu* Dieckmann et al. 1995). Other parameter: $s = 0.9$.

Figure 1



Local-adaptation trade-offs		Weak trade-offs	Moderately strong trade-offs	Very strong trade-offs
A Evolution of local adaptation under fixed and unconditional habitat choice				
Constant habitat outputs (Model 1)		Intermediate local adaptation 1 intermediate phenotype	Possible branching 2 specialists	Bistability 1 specialist
Variable habitat outputs (Models 2 and 3)			Bistability 1 specialist	
B Evolution of habitat choice under fixed and monomorphic local adaptation				
Local regulation (Models 1 and 3)		Intermediate habitat choice Ideal free distribution		
Global regulation (Model 2)		Maximal habitat choice One habitat remains empty		
C Joint evolution of local adaptation and habitat choice				
Constant habitat outputs (Model 1)	Local regulation (Models 1 and 3)	Branching 2 specialists		Bistability 1 specialist in ideal free distribution
Variable habitat outputs (Models 2 and 3)			Bistability 1 specialist in ideal free distribution	
	Global regulation (Model 2)	Bistability 1 specialist leaving the other habitat empty		

Figure 2

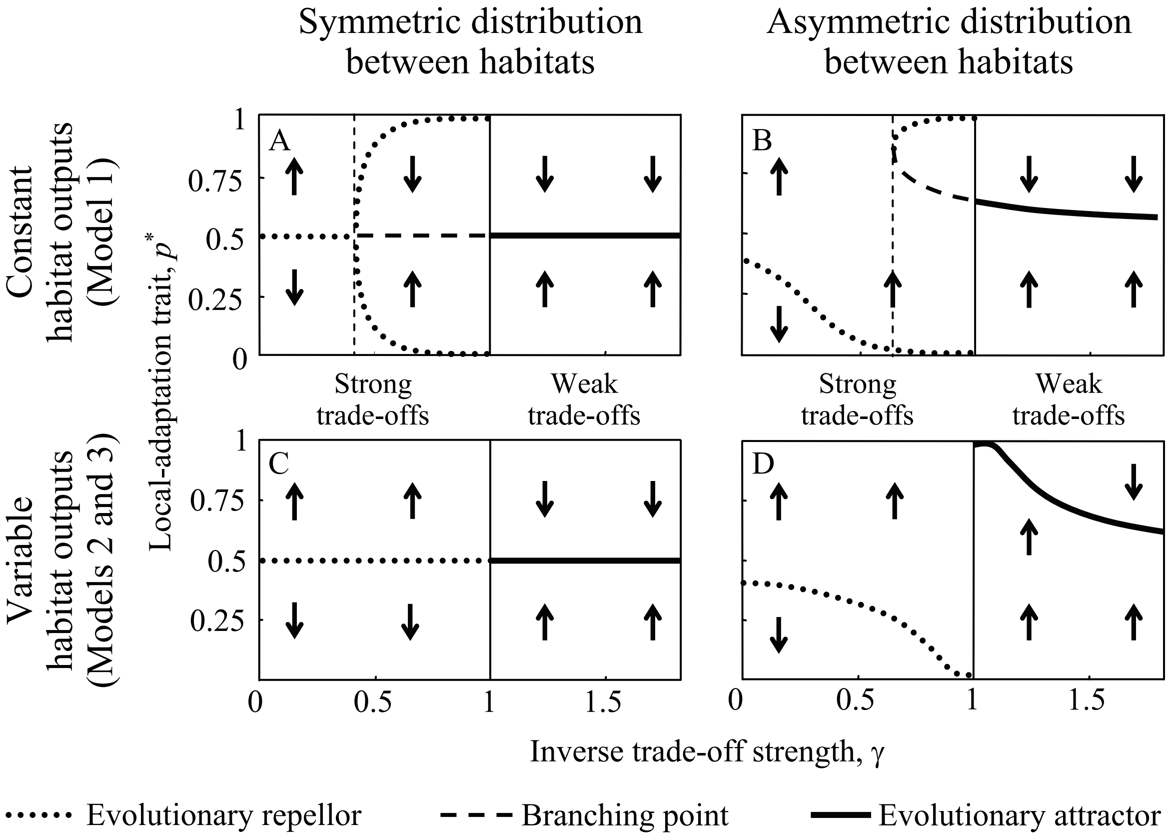

Symmetric distribution between habitats
Asymmetric distribution between habitats
Constant habitat outputs (Model 1)
Variable habitat outputs (Models 2 and 3)
Local-adaptation trait, p^*
A
B
C
D
1
0.75
0.5
0.25
0
Strong trade-offs
Weak trade-offs
0
0.5
1
1.5
Inverse trade-off strength, γ
Evolutionary repellor
Branching point
Evolutionary attractor

Figure 3

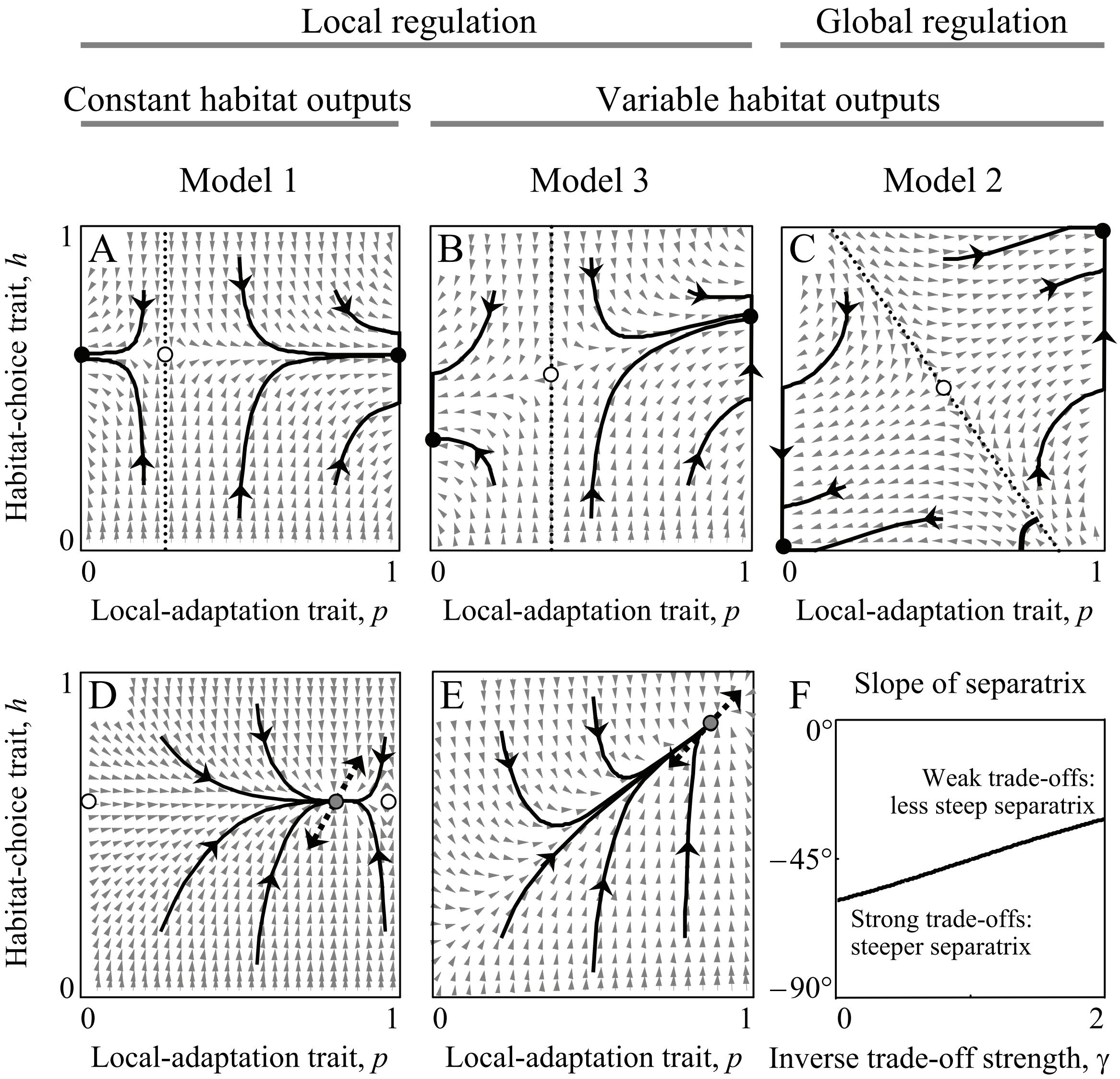

Local regulation
Global regulation
Constant habitat outputs
Variable habitat outputs
Model 1
Model 3
Model 2
A
B
C
D
E
F
Habitat-choice trait, *h*
Local-adaptation trait, *p*
0
1
Slope of separatrix
0°
−45°
−90°
Weak trade-offs: less steep separatrix
Strong trade-offs: steeper separatrix
0
2
Inverse trade-off strength, γ

Figure 4

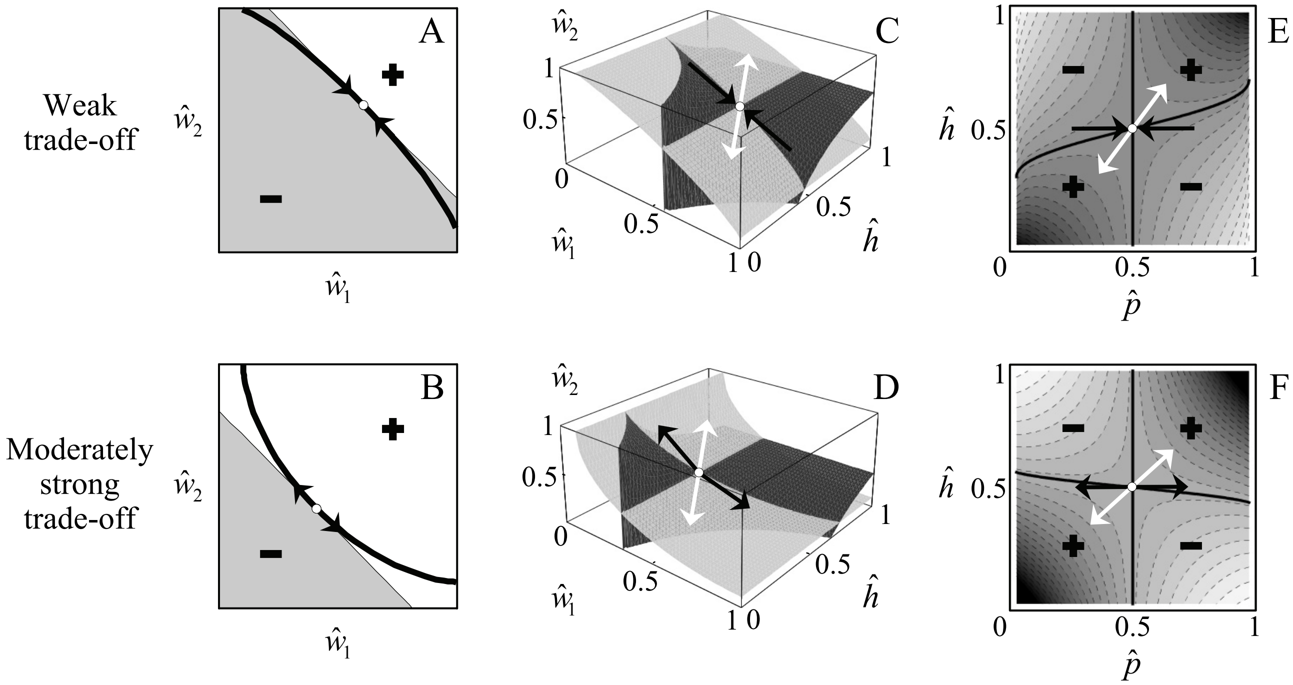
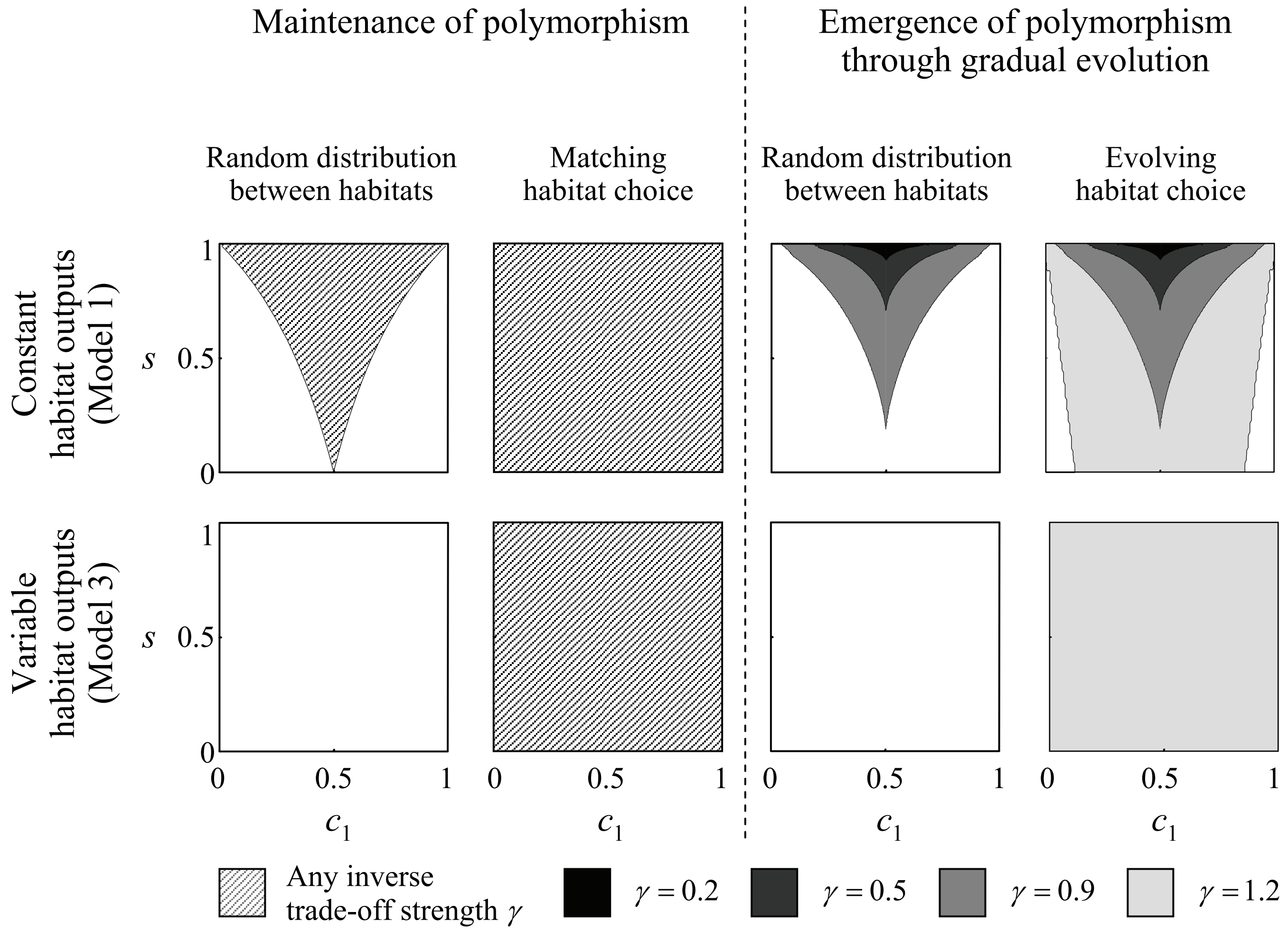

A
B
C
D
E
F
Weak trade-off
Moderately strong trade-off
$\hat{w}_1$
$\hat{w}_2$
$\hat{h}$
$\hat{p}$
0
0.5
1
+
−

Figure 5


Maintenance of polymorphism
Emergence of polymorphism through gradual evolution
Random distribution between habitats
Matching habitat choice
Random distribution between habitats
Evolving habitat choice
Constant habitat outputs (Model 1)
Variable habitat outputs (Model 3)
s
1
0.5
0
0
0.5
1
c_1
Any inverse trade-off strength γ
$\gamma = 0.2$
$\gamma = 0.5$
$\gamma = 0.9$
$\gamma = 1.2$

Appendix Figure 1