CHAPTER SEVEN

Dynamic patterns of adaptive radiation: evolution of mating preferences

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Introduction

Adaptive radiation is defined as the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Simpson 1953; Schluter 2000). Examples include the diversification of Darwin's finches on the Galápagos islands, *Anolis* lizards on Caribbean islands, Hawaiian silverswords, a mainland radiation of columbines, and cichlids of the East African Great Lakes, among many others (Simpson 1953; Givnish & Sytsma 1997; Losos 1998; Schluter 2000; Gillespie 2004; Salzburger & Meyer 2004; Seehausen 2006). Adaptive radiation typically follows the colonization of a new environment or the establishment of a 'key innovation' (e.g. nectar spurs in columbines, Hodges 1997) which opens new ecological niches and/or new paths for evolution.

Adaptive radiation is both spectacular and a remarkably complex process, which is affected by many different factors (genetical, ecological, developmental, environmental, etc.) interweaving in non-linear ways. Different, sometimes contradictory scenarios explaining adaptive radiation have been advanced (Simpson 1953; Mayr 1963; Schluter 2000). Some authors emphasize random genetic drift in small founder populations (Mayr 1963), while others focus on strong directional selection in small founder populations (Eldredge 2003; Eldredge *et al.* 2005), strong diversifying selection (Schluter 2000), or relaxed selection (Mayr 1963). Identifying the more plausible and general scenarios is a highly controversial endeavour. The large timescale involved and the lack of precise data on its initial and intermediate stages even make identifying general patterns of adaptive radiation very difficult (Simpson 1953; Losos 1998; Schluter 2000; Gillespie 2004; Salzburger & Meyer 2004; Seehausen 2006). Further, it is generally unknown if the patterns identified in specific case studies apply to other systems.

The difficulties in empirical studies of general patterns of adaptive radiation, its timescales, driving forces, and consequences for the formation of biodiversity make theoretical approaches important. Perhaps surprisingly, the phenomenon of adaptive radiation remains largely unexplored from a theoretical modelling perspective. Adaptive radiation can be viewed as an extension of

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the process of speciation (driven by ecological factors and subject to certain initial conditions) to larger temporal and spatial scales. A recent explosion in empirical speciation work (reviewed by Coyne & Orr 2004; Price 2008) has been accompanied by the emergence of a quantitative theory of speciation (Gavrilets 2004). In contrast, there have been few attempts to build genetically based models of large-scale evolutionary diversification. The few existing examples are applicable mostly to asexual populations or do not explicitly treat spatially heterogeneous selection and ecological competition but, instead, focus on stochastic factors (Hubbell 2001; Chow *et al.* 2004; Gavrilets 2004). However, it is thought that diversifying selection is very important in adaptive radiations, and adaptive diversification has been shown to overcome stochasticity and historical contingencies in similar environments (Losos *et al.* 1998). Therefore, diversifying, ecologically based selection needs to be explicitly incorporated into modelling approaches.

Recently, we (Gavrilets & Vose 2005) presented our initial attempts to build a realistic genetically explicit, individual-based model of adaptive radiation driven by ecological selection in a spatially heterogeneous environment. We were able to model evolutionary dynamics of populations with hundreds of thousands of sexual diploid individuals over a time span of 100 000 generations assuming realistic mutation rates and allowing for genetic variation in a large number of both selected and neutral loci. Our approach was built upon a model of speciation via adaptation to a new ecological niche occurring simultaneously with the evolution of genetically based preferences for the niche (Diehl & Bush 1989; Fry 2003). Although this model was originally proposed as a model of non-allopatric speciation in the apple maggot fly *Rhagoletis pomonella* (Feder 1998), it is applicable to other systems where individuals choose an ecological niche in which they mate and raise offspring. Besides its simplicity and generality, this model provides one of the easiest ways to achieve non-allopatric speciation (Gavrilets 2004). Furthermore, it is the only mathematical model of non-allopatric speciation strongly supported by experimental work (Rice & Salt 1990; Rice & Hostert 1993). We used this model within the framework of parapatric speciation (Coyne & Orr 2004; Endler 1977; Gavrilets 2003, 2004) in which spatial heterogeneity in selection, isolation by distance and migration into new patches all play critical roles. Our goal was to help identify potential general patterns of adaptive radiation and evaluate their characteristic timescales.

We consider a scenario in which a few individuals of a sexual diploid species colonize a new environment (e.g. an island or a lake) in which a number of spatially structured empty ecological niches are available. For example, *Anolis* radiation on Caribbean islands is largely driven by adaptation to six ecological niches associated with different parts of vegetation (Losos 1998). While the founders have low fitness, the abundant resources and lack of competitors allow them to seed a population that is able to survive throughout the environment at low densities. The founders have no particular preference for the ecological niches available in the new environment. However, as selection acts on the new genetic variation supplied by mutation, different lineages can become adapted to and simultaneously develop genetic preferences for different ecological niches. The process of ecological and phenotypic diversification driven by selection for local adaptation was accompanied by the growth in the densities of emerging species.

In this chapter, we start by outlining our model and then discuss its behaviour when mating remains random throughout the simulations (Gavrilets & Vose 2005). However, the evolution of mating preferences is a crucial factor in many speciation models and is strongly associated with reproductive isolation in empirical studies. Therefore, we examine next the evolution of non-random mating and its influence on the dynamics of reproductive isolation and diversification.

Mathematical model

We use a generalization of the model in Gavrilets and Vose (2005) which in turn generalizes and extends those in Diehl and Bush (1989), Johnson *et al.* (1996) and Fry (2003) (see also Kawecki 1996, 1997). The most important extension of our previous model concerns the incorporation of three additional traits controlling (non-random) mating (Gavrilets *et al.* 2007). We will use this model to study the process of invasion by a species into an environment where new ecological niches are available (Kawata 2002; Gavrilets & Vose 2005, 2007; Gavrilets *et al.* 2007). In the new environment, the invading species can be viewed as a low-fitness generalist. In contrast to most modelling work on evolution in a spatially heterogeneous environment which assumes *soft selection* (Kisdi & Geritz 1999; Spichtig & Kawecki 2004 and references therein, but see DeMeeus *et al.* 1993) and does not consider population densities explicitly, selection for local adaptation in our model is not only density-dependent but also *hard* (sensu Christiansen 1975). That is, the contribution of each niche to offspring depends on the fitness of individuals in the niche (which is more biologically realistic under the scenario we study). The following describes the major components of the model.

Space and environment

Space is subdivided into a rectangular array of ‘patches’ with each patch supporting a population of a certain size. For example, one can think of different parts of a lake environment, or different types of vegetation or soil. There are k environmental factors θ_i ($i = 1, 2, \ldots, k$). Each of these factors can take only two discrete values: 0 and 1, corresponding to two contrasting environmental conditions, such as sandy or rocky lake bottom, high or low light level, basalt or calcarenite soil, etc. Consequently, each patch belongs to one of 2^k possible types (‘ecological niches’). Initially, ecological niches are assigned to patches randomly with equal probabilities.

Individuals

Individuals are diploid. Each individual has a number of additive quantitative characters:

- k 'ecological' characters $x_1,\ldots, x_k$,
- k 'habitat preference' characters $y_1,\ldots, y_k$,
- three 'mating compatibility' characters m, f and c.

Ecological and habitat preference characters are expressed in both sexes. Following previous models (Dieckmann & Doebeli 1999; Bolnick 2004, 2006; Gavrilets *et al.* 2007) we assume that male display trait m is expressed in males only, whereas female mating preference traits f and c are expressed in females only. Trait f describes the value of the male trait that the female prefers most. Trait c characterizes the choosiness of the female. All these traits are scaled to [0,1] and are controlled by different unlinked diallelic loci with equal effects. Mutations occur at equal rates across all loci; the probabilities of forward and backward mutations are equal. In addition, there is a number of unlinked neutral loci with a large number of alleles subject to stepwise mutation (Ohta & Kimura 1973). These loci have higher mutation rates and are used to evaluate the levels of genetic divergence within and between species one would observe if using microsatellite markers.

Life-cycle

Generations are discrete and non-overlapping. The life cycle consists of the following stages, in order:

- density-dependent viability selection within the patch,
- preferential dispersal of surviving adults among neighbouring patches (including the patch of origin),
- non-random mating among individuals within the patch and offspring production.

Note that our description of the third stage implies that mating pairs are formed in the feeding habitat (e.g. as in many plant-feeding insects).

Viability selection

The i-th ecological character x_i controls the fitness component w_i associated with the i-th environmental factor. Specifically,

$$w_i = \exp\left[-\frac{(x_i-\theta_i)^2}{2\sigma_s^2}\right], \tag{1}$$

where θ_i is the optimum phenotype (which is given by the value of the i-th environmental factor in the niche). That is, each ecological character is subject to directional selection towards an extreme value (0 or 1). Parameter σ_s measures the strength of ecological selection; smaller values of σ_s mean stronger selection. The overall fitness w is taken to be the product of the fitness components (i.e. $w = w_1, w_2, \ldots, w_k$). Note that fitness of a 'specialist' (i.e. a genotype perfectly adapted to one niche) in a niche differing by j environmental factors ($j \leq k$) is $w_{j,\mathrm{spec}} = \exp[-j/(2\sigma_s^2)]$. Fitness of a 'generalist' (i.e. an individual with $x = 1/2$) is $w_{\mathrm{gen}} = \exp[-k/(8\sigma_s^2)]$ in all niches. Note that a hybrid between two individuals adapted to the two alternative states of an environmental factor will have an intermediate phenotype and low fitness in both environments (as implied in the scenario of ecological speciation (Schluter 2000; Forister 2005; Rundle & Nosil 2005)).

Within each patch selection acts on viability and is density dependent. The overall fitness w controls a carrying capacity, $K = K_0 w$, associated with the phenotype, where K_0 is the maximum carrying capacity (the same for all niches). The probability that an individual survives to the age of reproduction is given by the Beverton–Holt model (Kot 2001):

$$v = \frac{1}{1 + (b-1)\frac{N}{K}}, \tag{2a}$$

for monoecious individuals, and

$$v = \frac{1}{1 + (\frac{b}{2}-1)\frac{N}{K}}, \tag{2b}$$

for dioecious individuals, where $b > 0$ is a parameter (the average number of offspring per female; see below), and N is the number of juveniles in the patch.

Habitat preference and dispersal

The i-th preference character y_i controls preference component p_i for the i-th environmental factor. Preference component p_i is given by a linear function of y_i:

$$P_i = \frac{1}{2} \pm a_i\left(y_i - \frac{1}{2}\right),$$

where $0 \leq a_i \leq 1$ is a parameter measuring the maximum possible preference and the sign is '+' for $\theta_i = 1$ and '−' for $\theta_i = 0$. Note that if $y_i = 1/2$, the individual has equal preference for both states of the environmental factor (i.e. $p_i = 1/2$). The value of $1 - a_i$ can be interpreted as the probability that an individual with the highest preference for one habitat mistakenly goes to the other habitat. The overall preference for an ecological niche characterized by environmental factors $\theta_1, \theta_2, \ldots, \theta_k$ is taken to be the product of the individual preference components (i.e. $p = p_1, p_2, \ldots, p_k$). The probability that an adult enters a patch to mate and raise offspring is proportional to its preference p for the ecological niche present in the patch. Note that a hybrid between two individuals with strong preferences to the two alternative states of an environmental factor will have low preference for either environment (e.g. as experimentally demonstrated in species of maggot flies *Rhagoletis* where hybrids show reduced response to parental host-fruit odours (Linn *et al.* 2004)).

Each adult migrates to one of the eight neighbouring patches or returns back to its native patch with probabilities proportional to its preferences for the corresponding ecological niches. For patches at a boundary, the number of patches available for emigration is reduced according to the number of neighbouring patches.

Mating preference

The relative probability of mating between a female with traits f and c and a male with trait m is

$$\psi(m,f,c) = \begin{cases} \exp\left[-(2c-1)^2 \frac{(f-m)^2}{2\sigma_a^2}\right], \ \text{if}\, c > 0.5, \\ 1, \text{if}\, c = 0.5, \\ \exp\left[-(2c-1)^2 \frac{(f-(1-m))^2}{2\sigma_a^2}\right], \ \text{if}\, c > 0.5, \end{cases} \tag{3}$$

where parameter σ_a scales the strength of female mating preferences (Gavrilets *et al.* 2007). Under this parameterization, females with $c = 0.5$ mate randomly, females with $c > 0.5$ prefer males whose trait m is close to the female's trait f (positive assortative mating), and females with $c < 0.5$ prefer males whose trait m is close to $1 - f$ (negative assortative mating). Note that the absolute value $|2c - 1|$, which we will denote as C, characterizes the extent of deviation of the female's mate choice from random: females with $C = 0$ mate randomly while those with $C = 1$ exhibit the strongest possible (negative or positive) assortative mating. Parameter σ_a governs the width of the mating probability distribution; the small numerical value used below (0.1) implies that the mating preference loci have very strong effects on the probability of mating (Gavrilets *et al.* 2007).

Offspring production

Each mating results in a number of offspring drawn from a Poisson distribution with parameter b. We assume that all adult females mate. This assumption implies that any costs of mate choice, which can easily prevent divergence and speciation (Pomiankowski 1987; Bolnick 2004; Gavrilets 2004, 2005; Gourbiere 2004; Kirkpatrick & Nuismer 2004; Waxman & Gavrilets 2005), are absent. This assumption also means that the effective population size is increased relative to the actual number of adults (Gavrilets & Vose 2005).

Local extinction

At the start of every generation, each patch goes extinct with a small probability ε. When this happens, all individuals present there die and the 'niche' assigned to this patch is chosen anew randomly. The later assumption is a simple way to have some turnover of ecological niches. For example, if a patch represents a tree of a certain host species, then when the tree dies its space can be occupied by a tree of a different host species.

Reproductive isolation and species

We assume that genetic incompatibilities (Coyne & Orr 2004; Gavrilets 2004) are absent. Reproduction isolation can evolve in the model via differentiation in habitat preferences, selection against immigrants and hybridization, and sexual selection. In our model, for each individual, there is a niche, say niche J, where it is most fit, and there is a niche, say niche I, for which it has the strongest preference. We interpret each individual for whom $J = I$ as a member of 'ecological' species I. Each ecological species can be comprised by a number of 'sexual morphs' or 'sexual species', i.e. groups of individuals reproductively isolated by differences in mating preferences. Because fitness in a niche, preference for a niche and mating preferences are controlled genetically, our 'species' also represent distinguishable genetic clusters which are reproductively isolated to a certain degree (Mallet 1995; Pigliucci 2003). The degree of reproductive isolation gets progressively amplified as a by-product of ecological adaptation and strengthening of habitat and mating preferences.

Initial conditions

K_{init} adults populate a single patch in the upper left corner of the system. All individuals are identical homozygotes with all traits exactly at 1/2. Each microsatellite locus is heterozygous with two intermediate alleles out of 2^8 possible alleles.

Parameter values

We varied system size (8×8, 16×16, 32×32), number of loci per each trait ($L = 4$, 8, 16) and the local extinction rate ($\varepsilon = 0$, 0.0025, 0.01, 0.04). The following parameters did not change: number of traits $k = 3$, $\sigma_s = 0.356$ (which corresponds to the fitness of the generalists being 0.05 of the maximum possible value), average number of offspring $b = 4$, maximum strength of preference $a_i = 0.99$, number of 'microsatellite' loci $M = 8$ and mutation probability $\mu = 10^{-5}$ for the loci controlling ecological and preference traits and $\mu_n = 10^{-3}$ for the 'microsatellite' loci. 30–50 runs were done for each parameter combination. Simulations ran for up to 100 000–150 000 generations or until global extinction.

Population genetic structure at neutral loci

To estimate the levels of spatial structuring in neutral loci we used the AMOVA framework (Excoffier *et al.* 1992; Excoffier 2001).

Diversification under random mating

Here, we briefly summarize our previous results corresponding to the case when mating was forced to remain random throughout the simulations (Gavrilets & Vose 2005). In these simulations, individuals were monoecious, the number of founders was $K_{\text{init}} = 10$ individuals, and maximum carrying capacity was $K_0 = 500$ individuals. Under these conditions and for parameter combinations used in our numerical simulations, adaptive radiation into a number of ecological niches often follows the colonization of a new environment. Generally, in the course of the simulations, ecological traits evolve faster, approach their optimum trait values closer, and maintain less genetic variation at (stochastic) equilibrium than the habitat preference traits.

Area effect

In *Anolis* lizards, empty ecological niches get filled only on islands of sufficiently large area (Losos 1998). In our simulations, larger areas allow for more intensive diversification (see Figure 2 in Gavrilets & Vose 2005). For parameter values used, eight ecological niches are always available. However, in systems of smaller size (e.g. 8×8 or 16×16) not all niches are filled. The area effect has the following explanation. First, larger areas can support larger population sizes which in turn results in more advantageous mutants on which diversifying selection can act. Second and more importantly, in larger areas new locally advantageous genes may become better protected by distance from the diluting effect of locally deleterious genes, which otherwise can easily prevent adaptation to a new niche (Riechert 1993). Isolation by distance allows new advantageous combinations of genes to accumulate in large numbers, promoting further adaptations to new ecological niches.

Effect of the number of loci

In our simulations, increasing the number of loci underlying the traits decreases diversification (see Figure 2 in Gavrilets & Vose 2005). This happens because a larger number of loci implies weaker selection per each individual locus and a stronger overall effect of recombination in destroying coadapted gene complexes. Similar effects have been observed in a number of related models (Gavrilets 2004; Gavrilets & Vose 2007; Gavrilets *et al.* 2007).

Timing of speciation

Typically if more than one species emerges, there is a burst of speciation soon after colonization rather than a more or less continuous process of speciation (see Figure 3 in Gavrilets & Vose 2005). The explanation can be given in terms of ecological opportunity and genetic constraints (Erwin *et al.* 1987). Initially, the former is much larger (because there are more empty niches, local densities are low and competition is weaker), whereas the latter is much smaller (because the founders are not specialized) than later in the radiation. As a consequence, in our simulations more than 98% of speciation events occurred within the first 10 000 generations.

Overshooting effect

In some adaptive radiations, the diversity (i.e. the number of species) peaks early in the radiation. For example, the number of species of spiny-legged *Tetragnatha* spiders on younger Hawaii islands is larger than on the older ones (Gillespie 2004). Our simulations provide some support for the generality of this 'overshooting effect'. An explanation of the overshooting effect can be given in terms of the differences between the rates of species extinction and origination. Whereas the former is more or less constant in time (excluding the first few thousand generations), the latter decreases in time because of the effects of ecological opportunity and genetic constraints as discussed above. Note that the overshooting effect was system-size specific; it was not observed in 32 × 32 systems. The most likely reason is that larger systems require a longer period of time for a decline in diversity to become apparent.

Hybridization and neutral gene flow

In our simulations, species can stably maintain their divergence in a large number of selected loci for very long periods of time in spite of substantial hybridization and gene flow that removes differentiation in neutral markers. Similar observations are often made in natural populations. For example, blue butterfly species *Lycaeides idas* and *Lycaeides melissa* utilize different hosts and have diverged significantly in morphology, yet show no differentiation in neutral markers (Nice *et al.* 2002).

'Least action effect'

In our simulations, speciation occurring after the initial burst usually involves a change in a single pair of characters. This observation provides theoretical support for a prediction that shifts to radically different hosts will be much less common than shifts to similar hosts (Bush 1969). That is, if a host shift happens, it proceeds, metaphorically speaking, in the direction of least action. A related observation is that when some niches are not filled, the existing species differ in the minimum number of characteristics (1 or 2). These effects are explained by the fact that the deleterious effects of immigration of locally disadvantageous genes on the possibility of accumulation of locally advantageous genes become stronger with genetic difference between immigrating and resident genotypes.

Evolution of non-random mating

Next we consider individuals with discrete sexes and allow non-random mating to evolve. We have performed additional simulations varying the number *L* of loci per trait, the system size and the local extinction rate ε in the same way as in the previous section. Throughout the simulations we assumed that the carrying capacity was $K = 600$ individuals per deme; set parameter σ_a of the preference function (3) at 0.1; and started with 20 founders (10 males and 10 females). The founders were homozygous with ecological, habitat preference and mating preference traits all set at 0.5 for each individual. Thus, all founders were randomly mating generalists. For most parameter combinations, we accumulated 30 runs with the system surviving for about 100 000–150 000 generations. However, in systems of the smallest size (8×8) and with non-zero extinction rate, long-term survival was not observed (Gavrilets & Vose 2005). Figure 7.1 illustrates some states reached by the system with $k = 3$ (and, thus, eight possible ecological niches). In the four cases shown, 2, 8, 4 and 8 ecological niches were filled by two to three sexual species each. In the cases shown, a large number of local populations are close to the carrying capacity. However, in some patches populations are very small. These are 'sink populations' (Holt 1997) that cannot adapt to the conditions they experience because of the deleterious effect of migration of locally maladapted genotypes. A gallery of graphical results illustrating the final state of the system can be viewed at http://neko.bio.utk.edu/~avose/niche.

The overall dynamics were similar to those observed in the case of monoecious populations described above. However, because of an increased demographic stochasticity of dioecious populations, successful invasion was much less common. (That was actually the reason why we increased both the number of founders and the population carrying capacity relative to those used in the previous section.) The number of ecological niches filled during the diversification stage was reduced for the same reason.

Strength of non-random mating

The strength of non-random mating in the system can be characterized by the average value $\bar{C}$ of trait C ($= |2c - 1|$; see above) in the population. In our simulations, strong non-random mating does evolve often on the timescale studied. Tables 7.1 and 7.2 show the average time T taken for $\bar{C}$ to reach 0.5 for the first time. Also given there are the number of runs in which C did reach 0.5. Notice that time T is typically one order of magnitude larger than the characteristic time for the evolution of local adaptation and habitat preference (see above and Gavrilets & Vose 2005). Simulations also show C does not necessarily evolve to the maximum possible value but can be stably maintained at some intermediate values (cf. Matessi *et al.* 2001) or can drastically fluctuate in time (cf. Hayashi *et al.* 2007). Overall, the model predicts that partial sexual isolation (e.g. as between *Littorina* ecotypes (Rolán-Alvarez *et al.* 1997) or between *Timema* walking-stick ecotypes (Nosil *et al.* 2002)) should be common.

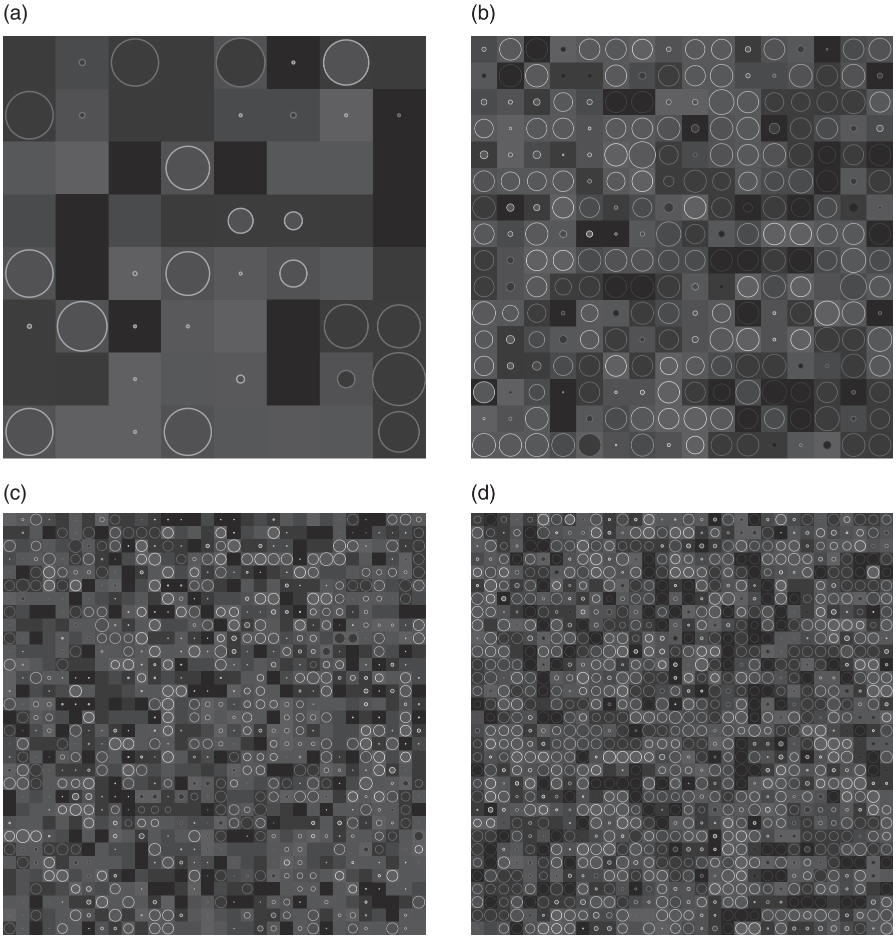

Figure 7.1 Examples of the system state with three environmental factors ($k = 3$, so that there are eight possible niches). Each square represents a patch. The colour of the square represents the ecological niche assigned to the patch. Each local population is represented by a circle. The radius of the circle is proportional to the population size (the maximum radius corresponds to a population at carrying capacity). The colour of the circle defines the niche preferred by the majority of individuals. Matching of the color of the corresponding square and circle (observed in most cases) means that the majority of individuals in the patch have preference for the ecological conditions they experience. (a) 8 × 8 systems with two ecological niches filled, (b) 16 × 16 system with eight ecological niches filled, (c) 32 × 32 system with four ecological niches filled, and (d) 32 × 32 system with eight ecological niches filled.

Drift versus selection (against hybridization)

In principle, non-random mating in our model can evolve by drift and/or selection against hybridization. Parameters of the model are expected to have much less effect on the dynamics of the processes if drift is more important than selection. The deleterious effect of hybridization is not present if only one

Table 7.1 *The average time to the evolution of non-random mating (in thousands of generations) over the runs with a single 'filled' niche*

		System size		
L	ε	8 × 8	16 × 16	32 × 32
4	0	61.6(4)	–	–
	0.0025	–	50.4(17)	–
	0.01	–	33.9(25)	–
	0.04	–	70.5(2)	–
8	0	84.8(5)	–	–
	0.0025	–	70.2(20)	–
	0.01	–	44.8(22)	–
	0.04	–	66.3(7)	–
16	0	113.1(4)	–	–
	0.0025	–	49.5(2)	–
	0.01	–	67.7(12)	–
	0.04	–	87.8(8)	–

Note: The number of runs is shown in the parentheses.

Table 7.2 *The average time to the evolution of non-random mating (in thousands of generations) over the runs with more than one 'filled' niches*

		System size		
L	ε	8 × 8	16 × 16	32 × 32
4	0	52.6(26)	39.0(30)	25.0(30)
	0.0025	–	25.5(13)	20.0(30)
	0.01	–	13.4(5)	20.8(30)
	0.04	–	32.2(28)	22.7(30)
8	0	92.4(13)	77.6(17)	83.8(15)
	0.0025	–	24.5(1)	65.9(26)
	0.01	–	33.5(1)	71.3(26)
	0.04	–	83.5(16)	69.4(28)
16	0	65.0(1)	69.0(1)	142.0(1)
	0.0025	–	121.1(1)	–
	0.01	–	73.5(1)	123.0(1)
	0.04	–	–	114.0(5)

Note: The number of runs is shown in the parentheses.

ecological niche is filled. Therefore, the runs in which C evolved to high values when only one ecological niche was filled (shown in Table 7.1) illustrate the evolution of non-random mating by drift. The runs in which C evolved to high values when more than one ecological niche was filled (shown in Table 7.2) can be interpreted as illustrating the evolution of non-random mating by selection against hybridization. Comparing Tables 7.1 and 7.2, one can see that non-random mating often evolved by drift in 16×16 systems, whereas this never happened in 32×32 systems. Table 7.2 shows that if selection against hybridization is present, non-random mating evolves faster in larger systems with fewer loci. Non-zero local extinction promotes the evolution of non-random mating (because local extinction causes turnover of populations, more contact between different ecological species, and more hybridization). However, provided local extinction rate ε is non-zero, the effect of its exact value seems to be small.

Divergence in mating characters

Evolution of non-random mating does not mean, by itself, divergence in mating characters between or within ecological species as mating preferences can be shared across different 'ecological species'. However, in the simulation we do observe both between- and within-(ecological) species divergence in mating preferences. Figure 7.2 shows examples of the distributions of mating characters observed in simulations with different number of ecological niches filled. For example, in case (a), two ecological niches are filled with two sexual species, each characterized by moderately strong negative assortative mating ($c < 0.5$). In case (d), all eight ecological niches are filled by three sexual species, each characterized by strong positive assortative mating ($c > 0.5$). In case (b), all eight ecological niches are filled by two sexual species; in each pair, one species exhibit strong positive assortative mating ($c > 0.5$) while the other species strong negative assortative mating ($c < 0.5$).

The distribution of mating characters often has a discrete nature. To charaterize this quantitatively, we defined the number of (sexual) morphs as the number of local maxima in the distribution of the male mating trait m observed after removing 'odd' trait values. For example, with $L = 4$ the possible trait values are 0, 1/8, 2/8, 3/8, 4/8, 5/8, 6/8, 7/8 and 8/8. After removal of 'odd' values, we are left with five 'even' values 0, 2/8, 4/8, 6/8 and 8/8. Simulations strongly suggest that 'even' values capture the internal cluster structure of the population much better than the 'odd' ones (because peaks in the distribution of the male trait m at 'odd' numbers often represent hybrids). Table 7.3 shows the number of sexual morphs (or 'sexual species') at the end of the run per filled ecological niche. In simulations, we have observed up to 3–4 distinct sexual morphs per ecological species and up to 24 discrete reproductively isolated species. However, in some cases, we observed an almost uniform distribution of the male trait m rather than discrete clusters or 'peaks' (see Fig. 7.2).

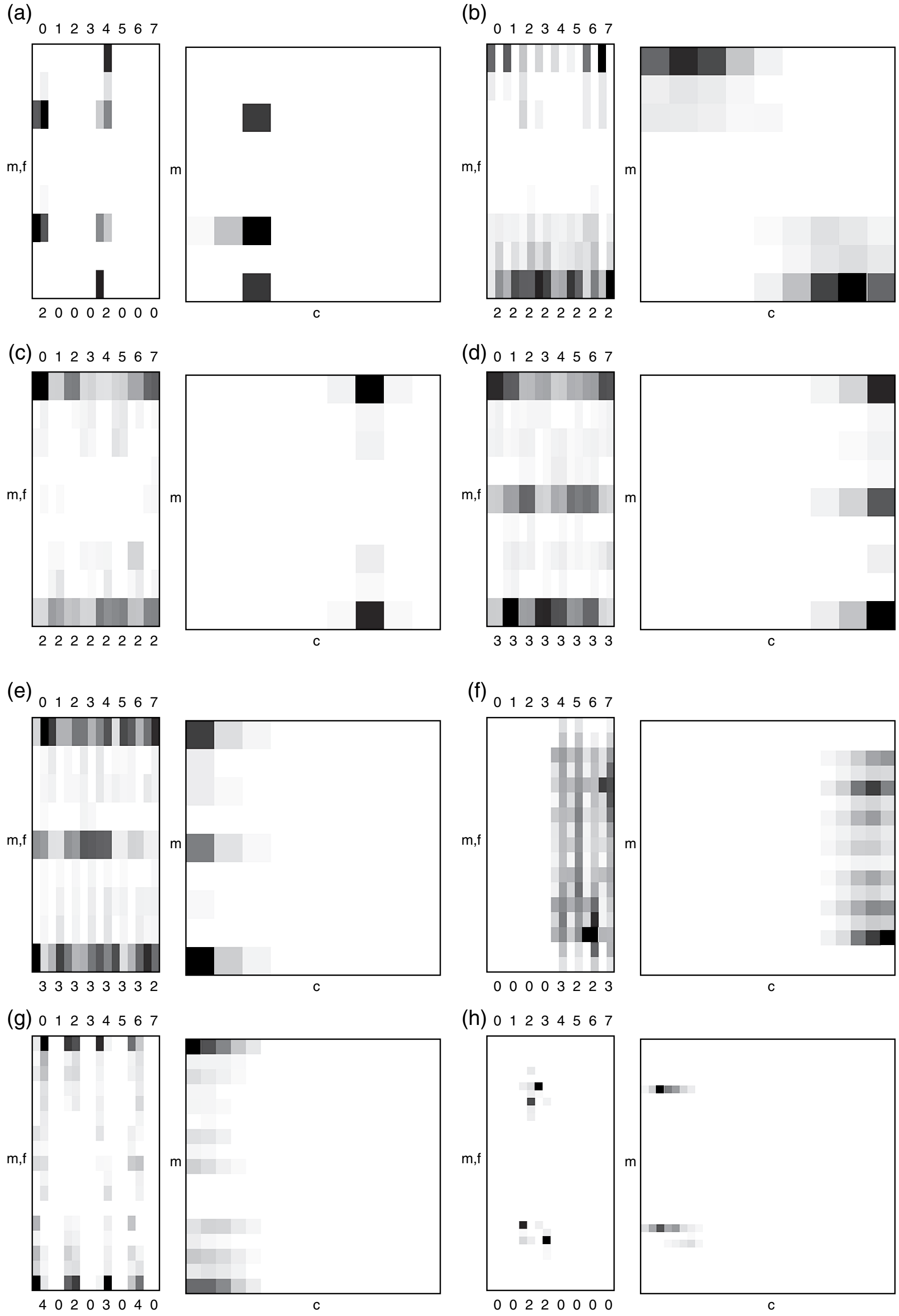

Figure 7.2 Examples of the distributions of mating characters across different ecological niches and overall in the system. The first graph in each pair shows the distributions of male display trait (m; left bar for each niche) and female preference trait (f; right bar for each niche) within each of the eight niches (0,1, …, 7). The traits change between 0 (upper boundary of the graph) and 1 (lower boundary of the graph). The intensity of the black

Table 7.3 *Average number of mating morphs per 'filled' ecological niche at the end of simulations*

		System size		
L	ε	8 × 8	16 × 16	32 × 32
4	0	1.31	1.89	1.97
	0.0025	–	1.42	2.62
	0.01	–	1.00	2.48
	0.04	–	1.10	2.26
8	0	1.26	1.63	2.05
	0.0025	–	1.16	2.35
	0.01	–	1.10	1.58
	0.04	–	1.00	1.24
16	0	1.31	1.63	1.78
	0.0025	–	1.33	1.36
	0.01	–	1.16	1.15
	0.04	–	1.00	1.13

Table 7.4 shows an alternative diversity index γ for the male traits which we defined as twice the standard deviation of trait m in the population. This index can take values between zero and one with the latter being observed when the distribution is symmetric bimodal with peaks at 0 and 1. In both cases, we chose to work with male character m rather than female characters f and c because males are under (sexual) selection whereas female traits can evolve more or less randomly/neutrally (at least as long as selection against hybridization is not too strong).

Figure 7.1 color is proportional to the frequency of individuals with the corresponding trait value. The numbers at the bottom give the number of 'sexual morphs' per each ecological niche. The second graph in each pair shows the overall distribution of male display trait (m) versus the overall distribution of female mating tolerance trait c. The traits change between 0 (upper left corner of the graph) and 1 (lower right corner of the graph). The intensity of the black colour is proportional to the frequency of individuals with the corresponding trait value. Shown are: (a) run 11 in set 0 (8×8, $L = 4$, $\varepsilon = 0$, 2 filled niches), (b) run 6 in set 12 (16×16, $L = 4$, $\varepsilon = 0$, 8 filled niches), (c) run 23 in set 12 (16×16, $L = 4$, $\varepsilon = 0$, 8 filled niches), (d) run 12 in set 25 (32×32, $L = 4$, $\varepsilon = 0.0025$, 8 filled niches), (e) run 13 in set 25 (32×32, $L = 4$, $\varepsilon = 0.0025$, 8 filled niches), (f) run 0 in set 29 (32×32, $L = 8$, $\varepsilon = 0.0025$, 4 filled niches), (g) run 9 in set 29 (32×32, $L = 8$, $\varepsilon = 0.0025$, 4 filled niches) and (h) run 6 in set 35 (32×32, $L = 16$, $\varepsilon = 0.04$, 2 filled niches). Note that when mating is positive assortative (so that $c > 0.5$; cases c, d, f and, partially, b) the distributions of m and f are fairly similar; if mating is negative assortative (so that $c < 0.5$; the rest of the cases), the distribution of m is a mirror image of the distribution of f around 1/2. See http://neko.bio.utk.edu/~avose/niche for a compete gallery of graphical results.

Table 7.4 *Average diversity γ in the male mating character* m *at the end of simulations ($0 \leq \gamma \leq 1$)*

		System size		
L	ε	8 × 8	16 × 16	32 × 32
4	0	0.47	0.82	0.79
	0.0025	–	0.47	0.84
	0.01	–	0.07	0.83
	0.04	–	0.13	0.82
8	0	0.17	0.33	0.53
	0.0025	–	0.12	0.77
	0.01	–	0.06	0.59
	0.04	–	0.05	0.65
16	0	0.08	0.14	0.16
	0.0025	–	0.08	0.11
	0.01	–	0.06	0.08
	0.04	–	0.03	0.08

Importantly, throughout the simulations there is much more variation in female mating preference traits than in the male traits (because there is no cost of choosiness for females, but males are often subject to strong sexual selection). Both Tables 7.3 and 7.4 show that diversification in male mating character is more extensive if the number of loci and the local extinction rate are small but the system size is large. That is, the qualitative effects of these parameters on the diversification in mating characters are the same as on the diversification in ecological characters.

Does more ecological species mean more sexual species?

Whether species diversity promotes speciation is a controversial topic (Cadena *et al.* 2005; Emerson & Kolm 2005). Does ecological diversification per se promote the evolution of non-random mating in our simulations? To answer this question, we calculated the correlation between the number of ecological niches filled at the moment when C reached 1/2 for the first time (which can be viewed as a measure of ecological diversity at speciation) and the following four variables: (1) T (i.e. the time to $C = 0.5$), (2) the number of sexual morphs per filled niche, (3) diversity index γ, and (4) the value of C. The last three variables were evaluated at the end of simulations. To save space, rather than giving four different tables with correlations and marking statistically significant correlations with, say, stars we decided to collect all statistically significant correlations in a single table (Table 7.5). This table suggests that more filled ecological

Table 7.5 *Significant correlations (at* P = *0.05) of measures of sexual diversification with the number of filled niches at* C = *0.5*

		System size		
L	ε	8 × 8	16 × 16	32 × 32
4	0	+1		
	0.0025		+2,3,4	−1
	0.01		−1	−1
	0.04		−1	−1 + 3
8	0			+3
	0.0025			+2
	0.01			−1 + 2
	0.04			
16	0			
	0.0025		+1	
	0.01			
	0.04			

Note: Plus signifies positive correlation and minus negative. The numbers correspond to the correlations with (1) T (i.e. the time to $C = 0.5$), (2) the number of sexual morphs per filled niche, (3) diversity index γ, and (4) the value of C. Empty spots mean statistically insignificant correlations.

niches sometimes result in shorter times to the evolution of non-random mating, more sexual morphs, larger diversity in male characters and larger strength of non-random mating. However, these effects are not necessarily strong.

The role of reinforcement

A standard argument in evolutionary biology is that a contact between populations adapted to different ecological niches will result in their divergence in mating characters so that the effects of hybridization and resulting deleterious gene flow between them are reduced.

This is a classical reinforcement scenario supported by data and a number of mathematical models (Butlin 1987, 1995; Howard 1993; Servedio & Noor 2003; Coyne & Orr 2004; Gavrilets 2004). How common is between-niche diverge in mating characters without within-niche diversification in our simulations? The surprising answer is that ‘classical’ reinforcement is not common at all. Overall, with two ecological niches filled, strong reproductive isolation (with $C > 0.5$ and $\gamma > 0.5$) has evolved in 40 runs under eight different sets of parameters. Within-niche diversification was absent in only four of these cases (under two different sets of parameters). With four ecological niches filled, strong reproductive isolation (with $C > 0.5$ and $\gamma > 0.5$) has evolved in more than 130 runs under 13 different sets of parameters. Within-niche diversification was absent in only 13 of these cases (under two different sets of parameters). These results can be understood in the following terms. The populations occupying and adapted to different ecological niches do start diverging in mating characters upon a contact (as postulated in the reinforcement scenario). However, reproductive isolation between them is never strong initially. Therefore, whatever new mating traits emerge in one ecological niche readily spread across the (ecological) species boundary and become represented in other ecological niches. Such 'parallel' diversification in mating characters does result in a reduction of gene flow between different ecological niches, some between-niche gene flow is maintained. Simultaneously, 'parallel' diversification creates within-niche divergence in mating characters and reduction in within-niche gene flow. At least in the model studied here, the classical reinforcement appears to be a short-term process.

Previous modelling work on reinforcement has never been performed at the level of complexity and biological realism used here. This probably explains why the within-species diversification in mating characters accompanying reinforcement has not been identified earlier.

The role of hybridization

Recently, there has been a lot of interest in hybridization in natural populations (Rieseberg 1995, 1999; Arnold 1997; Dowling and Secor 1997; Barton 2001) with some researchers forcefully arguing for a very important role of hybridization in biological diversification, speciation and adaptive radiation of not only plants but also animals (Seehausen 2004; Arnold & Meyer 2006; Mavarez *et al.* 2006; Mallet 2007). Is there a role for hybridization in this model? In the previous subsection, we already discussed the phenomenon of parallel diversification in mating characters which occurs as a result of hybridization following the emergence of new mating traits. A similar behaviour occasionally occurs with regard to ecological traits. In most modelled cases, all species observed at the end of a simulation run originate more or less simultaneously (see also Gavrilets and Vose (2005)). However, occasionally new ecological species originate significantly after the initial diversification. In such a case, the new ecological trait spreads across the species boundary, which results in essentially doubling the number of species in the system. We note that these dynamics (e.g. rapid emergence of multiple species after an extended period of stable species diversity) resemble those emphasized by punctuated equilibrium theory (Eldredge 1971; Eldredge & Gould 1972; Gould 2002).

In our simulations, different species are never completely isolated geographically, and it is impossible for different species to accumulate significant divergence without recombinant genotypes and species being quickly present. However, if one starts, say, with just two species diverged in all three ecological and all three habitat preference characters, hybridization between them can rapidly result in six additional ecological species. The importance and plausibility of this process will depend on the strength of selection for local adaptation and the strength of non-random mating present prior to the hybridization event. We have not yet explored these factors systematically.

Local adaptation and speciation

In our model, more (ecological) species typically means less local adaptation for each individual species. This happens because more species implies more opportunities for hybridization, the consequence of which is locally deleterious gene flow. The correlations between fitness and the number of ecological niches filled and between fitness and the overall number of species present are consistently negative and in many cases are statistically significant.

Stages of diversification

Simulations show that diversification in the model usually occurs in a particular order. First, populations diverge in ecological traits; second, in habitat preferences; and, third, in mating characters. Unless there is a global extinction, the first two steps are observed always and typically occur within several thousand generations after the founders enter the new environment. The first two steps are usually separated by several hundred generations but, rarely, occur one or two thousand generations apart. The third step is not guaranteed. If it does occur, it usually happens tens of thousands of generations after the first two steps. Diversification in mating characters usually occurs in parallel in different ecological niches. Only rarely do new ecological niches become colonized significantly after the initial bout of diversification. In this case, most mating characters quickly become represented in the new niche. Overall, diversification occurs in pulses.

Discussion

Here, we have described an explicit genetic model of adaptive radiation driven by selection for adaptation to discrete multivariate ecological niches. We have shown that strong ecologically based spatially heterogeneous selection coupled with limited migration, genetically based habitat choice and genetically based mate choice can indeed result in rapid phenotypic and ecological diversification and the emergence of multiple species reproductively isolated by a variety of mechanisms (local adaptation, habitat and mating preferences).

In our model, ecological traits evolve faster, approach their optimum trait values closer, and maintain less genetic variation at (stochastic) equilibrium than the habitat preference traits. Mating preference traits evolve slower than the other two sets of traits, maintain more genetic variation, and can fluctuate dramatically in time. Mating preferences can diverge both between and within species utilizing different ecological niches.

Our earlier work (Gavrilets & Vose 2005) has already provided strong theoretical support, clarification and explanation for a number of patterns of adaptive radiation including the area effect, the overshooting effect and the least action effect. It also suggested that diversification is strongly promoted if genetics underlying the traits involved are simple and most speciation events occur soon after colonization of a new environment while the rest occur mostly in pulses. We also showed that species can stably maintain their divergence in a large number of selected loci for very long, effectively infinite, periods of time in spite of substantial hybridization and gene flow that removes differentiation in neutral markers. The latter observation strongly supports the idea that genomes can be rather porous (Feder 1998; Wu 2001). The new results presented here support the generality of all these earlier conclusions.

Our new model shows that non-random mating can often evolve. With a non-negligible probability, it can happen by mutation and random drift alone (Gavrilets 2004). As expected, selection against hybridization dramatically increases the likelihood of evolution of strong non-random mating. However, there are a couple of underappreciated patterns. First, reproductive isolation is almost never absolute, and some hybridization and gene flow are always happening. As a result, neutral alleles can pass between different species. Second, this gene flow also results in sharing mating characters (especially during the initial stages when non-random mating is not strong yet) and, less commonly, ecological characters across species boundaries. These processes produce parallel speciation when new mating characters get shared across different ecological niches and/or new ecological characters get shared across different 'sexual morphs'. Third, these processes result in within-niche differentiation in mating preference and in emergence of sister species. Fourth, the model demonstrates that while ecological characters and habitat preference are rather stable in time, traits involved in mating are very dynamic and often vary dramatically both in time and in space. A related observation is that differentiation in mating characters is often of more a continuous nature with clearly defined discrete morphs not necessarily present.

Both the existing empirical data and theory show that genetic, ecological and environmental details have profound effects on the dynamics of speciation and diversification and that no universal rules of speciation exist. At the same time, one should expect that some relatively common trends or tendencies of evolutionary diversification in related groups of organisms can be identified. For example, in birds of the New Guinea mountains the diversification with respect to habitat elevation preceded diversification with respect to other characteristics (Diamond 1986; Schluter 2000; but see Price 2008 for an alternative interpretation). In some fishes, birds, and lizards, a common sequence of events in evolutionary diversification is divergence, first, in habitat, then in food type, and, finally, in mating signals (Streelman & Danley 2003). Earlier, analysis of various speciation models (Gavrilets 2004) has suggested that the following sequence of diversification events should be typically observed: (1) divergence with respect to macrohabitat, (2) evolution of microhabitat choice and divergence with respect to microhabitat, (3) divergence with respect to 'magic traits' (i.e. traits that control simultaneously the degree of local adaptation and non-random mating), and (4) divergence with respect to other traits controlling survival and reproduction. The model studied here does not differentiate between microhabitat and macrohabitat and does not include 'magic traits'. However, it does show that divergence in mating characters occurs much later than divergence in traits that control adaptation to and preference for habitat and, thus, provides partial support for the arguments above.

We note that some of the patterns discussed here have been identified previously in specific biological systems. However, the generality of these patterns cannot be assured on the basis of single cases that are known currently.

The fact that we were able to reproduce these macroevolutionary patterns starting with microevolutionary processes of mutation, random drift, migration, recombination and selection strongly support the generality of these patterns. We expect that these patterns will be observed in most adaptive radiations. Besides being able to capture the essence of adaptive radiation qualitatively, the model studied here allows one to make some quantitative conclusions on the important timescales of diversification, the number of species likely to emerge, and the effects of various parameters.

Due to computing power limitations, we varied only a limited number of parameters. Here we briefly discuss the expected effects of changing other parameters and assumptions (see also Gavrilets 2004; Gavrilets & Vose 2005). For the parameter values used here, no generalists ever survived competition against specialists. Weaker selection for local adaptation may, however, result in generalists being the most dominant type (see Gavrilets & Vose 2007; Gavrilets *et al.* 2007). Reduced probability of leaving the patch will make divergence slower (because selection against immigrants from diverged habitats will be less effective). Assuming non-equal allelic effects will constrain divergence in mating characters and result in fewer species (because the loci with smaller effects will be less responsive to selection and, thus, will diverge to a smaller degree). The loci with larger effects are expected to diverge first. Introducing costs of being choosy will significantly reduce or completely prevent divergence in mating characters. Linkage will result in differential genetic divergence across parts of genome with genes closely linked to selected loci being more differentiated than loosely linked genes. As a result, diverged genes will tend to form clusters (Wu 2001; Emelianov *et al.* 2004; Gavrilets 2004). Allowing for other forms of reproductive isolation (e.g. genetic incompatibilities) to evolve is not expected to change dramatically the patterns discussed above because they will evolve at much slower rates than ecological traits, habitat preferences and mating characters (Gavrilets 2004). We also note that assuming environmental factors are distributed along gradients rather than randomly does not seem to reduce neutral gene flow between emerging species (Gavrilets & Vose unpublished).

The current explosive growth in empirical knowledge on different aspects of speciation and adaptive radiation should soon make it possible to evaluate the generality and relevance of the patterns identified here and test the predictions made.

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References

Arnold, M. L. (1997) *Natural Hybridization and Evolution*. Oxford University Press, Oxford.

Arnold, M. and Meyer, A. (2006) Natural hybridization in primates: one evolutionary mechanism. *Zoology* **109**, 261–276.

Barton, N. H. (2001) The role of hybridization in evolution. *Molecular Ecology* **10**, 551–568.

Bolnick, D. (2004) Waiting for sympatric speciation. *Evolution* **58**, 895–899.

Bolnick, D. (2006) Multi-species outcomes in a common model of sympatric speciation. *Journal of Theoretical Biology* **241**, 734–744.

Bush, G. (1969) Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* **23**, 237–251.

Butlin, R. (1987) Speciation by reinforcement. *Trends in Ecology and Evolution* **2**, 8–13.

Butlin, R. K. (1995) Reinforcement: an idea evolving. *Trends in Ecology and Evolution* **10**, 432–434.

Cadena, C. D., Ricklefs, R. E., Jimenez, I. and Bermingham, E. (2005) Is speciation driven by species diversity? *Nature* **438**, E1–E2.

Chow, S. S., Wilke, C. O., Ofria, C., Lenski, R. E. and Adami, C. (2004) Adaptive radiation from resource competition in digital organisms. *Science* **305**, 84–86.

Christiansen, F. (1975) Hard and soft selection in a subdivided population. *American Naturalist* **109**, 11–16.

Coyne, J. and Orr, H. A. (2004) *Speciation*. Sinauer Associates, Inc., Sunderland, MA.

DeMeeus, T., Michalakis, Y., Renaud, F. and Olivieri, I. (1993) Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation – soft and hard selection models. *Evolutionary Ecology* **7**, 175–198.

Diamond, J. (1986) Evolution of ecological segregation in the New Guinea mountane avifauna. In: *Community Ecology* (ed. J. Diamond and T. J. Case), pp. 98–125. Harper and Row, Publishers, New York.

Dieckmann, U. and Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature* **400**, 354–357.

Diehl, S. R. and Bush, G. L. (1989) The role of habitat preference in adaptation and speciation. In: *Speciation and Its Consequences* (ed. D. Otte and J. A. Endler), pp. 345–365. Sinauer, Sunderland, MA.

Dowling, T. and Secor, C. (1997) The role of hybridization and introgression in the diversification of animals. *Annual Review of Ecology and Systematics* **28**, 593–619.

Eldredge, N. (1971) The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* **25**, 156–167.

Eldredge, N. (2003) The sloshing bucket: how the physical realm controls evolution. In: *Towards a Comprehensive Dynamics of Evolution:*

Exploring the Interplay of Selection, Neutrality, Accident, and Function (ed. J. Crutchfield and P. Schuster), pp. 3–32. Oxford University Press, New York.

Eldredge, N. and Gould, S. J. (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: *Models in Paleobiology* (ed. T. J. Schopf), pp. 82–115. Freeman, Cooper, San Francisco.

Eldredge, N., Thompson, J. N., Brakefield, P. M., *et al.* (2005) Dynamics of evolutionary stasis. *Paleobiology* **31**, 133–145.

Emelianov, I., Marec, F. and Mallet, J. (2004) Genomic evidence for divergence with gene flow in host races of the larch budmoth. *Proceedings of the Royal Society London B* **271**, 97–105.

Emerson, B. and Kolm, N. (2005) Species diversity can drive speciation. *Nature* **434**, 1015–1017.

Endler, J. A. (1977) *Geographic Variation, Speciation and Clines*. Princeton University Press, Princeton, NJ.

Erwin, D. H., Valentine, J. W. and Sepkoski, J. J. (1987) A comparative study of diversification events: the early Paleozoic versus the Mesozoic. *Evolution* **41**, 1177–1186.

Excoffier, L. (2001) Analysis of population subdivision. In: *Handbook of Statistical Genetics* (ed. D. J. Balding, M. Bishop and C. Cannings), pp. 271–307. John Wiley & Sons, Ltd, chichester, UK.

Excoffier, L., Smouse, P. and Quattro, J. (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* **131**, 479–491.

Feder, J. L. (1998) The apple maggot fly, *Rhagoletis pomonella*: flies in the face of conventional wisdom about speciation? In: *Endless Forms: Species and Speciation* (ed. D. J. Howard and S. H. Berlocher), pp. 130–144. Oxford University Press, New York.

Forister, M. L. (2005) Independent inheritance of preference and performance in hybrids between host races of Mitoura butterflies. *Evolution* **59**, 1149–1155.

Fry, J. D. (2003) Multilocus models of sympatric speciation: Bush versus Rice versus Felsenstein. *Evolution* **57**, 1735–1746.

Gavrilets, S. (2003) Models of speciation: what have we learned in 40 years? *Evolution* **57**. 2197–2215.

Gavrilets, S. (2004) *Fitness Landscapes and the Origin of Species*. Princeton University Press, Princeton, NJ.

Gavrilets, S. (2005) ‘Adaptive speciation’: it is not that simple. *Evolution* **59**, 696–699.

Gavrilets, S. and Vose, A. (2005) Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 18040–18045.

Gavrilets, S. and Vose, A. (2007) Case studies and mathematical models of ecological speciation. 2. Palms on an oceanic island. *Molecular Ecology* **16**, 2910–2921.

Gavrilets, S., Vose, A., Barluenga, M., Salzburger, W. and Meyer, A. (2007) Case studies and mathematical models of ecological speciation. 1. Cichlids in a crater lake. *Molecular Ecology* **16**, 2893–2909.

Gillespie, R. (2004) Community assembly through adaptive radiation. *Science* **303**, 356–359.

Givnish, T. and Sytsma, K. (1997) *Molecular Evolution and Adaptive Radiation*. Cambridge University Press, Cambridge.

Gould, S. J. (2002) *The Structure of Evolutionary Theory*. Harvard University Press, Boston.

Gourbiere, S. (2004) How do natural and sexual selection contribute to sympatric speciation? *Journal of Evolutionary Biology* **17**, 1297–1309.

Hayashi, T. I., Vose, M. D. and Gavrilets, S. (2007) Genetic differentiation by sexual conflict. *Evolution* **61**, 516–529.

Hodges, S. (1997) A rapid adaptive radiation via a key innovation in aquilegia. In: Molecular evolution and adaptive radiations. In: *Molecular Evolution and Adaptive Radiations* (ed. T. Givinish and K. Sytsma), pp. 391–405. Cambridge University Press, Cambridge.

Holt, R. D. (1997) On the evolutionary stability of sink populations. *Evolutionary Ecology* **11**, 723–731.

Howard, D. J. (1993) Reinforcement: origin, dynamics, and fate of an evolutionary hypothesis. In: *Hybrid Zones and the Evolutionary Process* (ed. R. G. Harrison), pp. 46–69. Oxford University Press, New York.

Hubbell, S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Johnson, P. A., Hoppensteadt, F. C., Smith, J. J. and Bush, G. L. (1996) Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortative mating. *Evolutionary Ecology* **10**, 187–205.

Kawata, M. (2002) Invasion of empty niches and subsequent sympatric speciation. *Proceedings of the Royal Society London B* **269**, 55–63.

Kawecki, T. J. (1996) Sympatric speciation driven by beneficial mutations. *Proceedings of the Royal Society London B* **263**, 1515–1520.

Kawecki, T. J. (1997) Sympatric speciation via habitat specialization driven by deleterious mutations. *Evolution* **51**, 1751–1763.

Kirkpatrick, M. and Nuismer, S. L. (2004) Sexual selection can constrain sympatric speciation. *Proceedings of the Royal Society London B* **271**, 687–693.

Kisdi, E. and Geritz, S. A. H. (1999) Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in heterogeneous environment. *Evolution* **53**, 993–1008.

Kot, M. (2001) *Elements of Mathematical Ecology*. Cambridge University Press, Cambridge.

Linn, C. E., Dambroski, H. R., Feder, J. L., *et al.* (2004) Postzygotic isolating factor in sympatric speciation in *Rhagoletis* flies: reduced response of hybrids to parental host-fruit odor. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 17753–17758.

Losos, J. B. (1998) Ecological and evolutionary determinants of the species-area relationship in Carribean anoline lizards. In: *Evolution on Islands* (ed. P. Grant), pp. 210–224. Oxford University Press, Oxford.

Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K. and Rodriguez-Schettino, L. (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118.

Mallet, J. (1995) A species definition for the modern synthesis. *Trends in Ecology and Evolution* **10**, 294–299.

Mallet, J. (2007) Hybrid speciation. *Nature* **446**, 279–283.

Matessi, C., Gimelfarb, A. and Gavrilets, S. (2001) Long term buildup of reproductive isolation promoted by disruptive selection: how far does it go? *Selection* **2**, 41–64.

Mavarez, J., Salazar, C., Bermingham, E., *et al.* (2006). Speciation by hybridization in Heliconius butterflies. *Nature* **441**, 868–871.

Mayr, E. (1963) *Animal Species and Evolution*. Belknap Press, Cambridge, MA.

Nice, C. C., Fordyce, J. A., Shapiro, A. M. and French-Constant, R. (2002) Lack of evidence for reproductive isolation among ecologically specialized lycaenid butteflies. *Ecological Entomology* **27**, 702–712.

Nosil, P., Crespi, B. J. and Sandoval, C. P. (2002) Host-plant adaptation drives the parallel evolution of reproductive isolation. *Nature* **417**, 440–443.

Ohta, T. and Kimura, M. (1973) A model of mutation appropriate to estimate the number of electrophoretically detectable alleles in a finite population. *Genetical Research* **22**, 201–204.

Pigliucci, M. (2003) Species as family resemblance concepts: the (dis-)solution of the species problem? *Bioessays* **25**, 596–602.

Pomiankowski, A. (1987) The costs of choice in sexual selection. *Journal of Theoretical Biology* **128**, 195–218.

Price, T. (2008) *Speciation in Birds*. Roberts and Company, Greenwood Village, CO.

Rice, W. R. and Hostert, E. E. (1993) Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* **47**, 1637–1653.

Rice, W. R. and Salt, G. (1990) The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution* **44**, 1140–1152.

Riechert, S. E. (1993) Investigation of potential gene flow limitation of behavioral adaptation in an aridland spider. *Behavioral Ecology and Sociobiology* **32**, 355–363.

Rieseberg, L. H. (1995) The role of hybridization in evolution: old wine in new skins. *American Journal of Botany* **82**, 944–953.

Rieseberg, L. H. (1999) Hybrid origin of plant species. *Annual Review of Ecology and Systematics* **28**, 359–389.

Rolán-Alvarez, E., Johannesson, K. and Erlandson, J. (1997) The maintenance of a cline in the marine snail *Littorina Saxatilis*: the role of home site advantage and hybrid fitness. *Evolution* **51**, 1838–1847.

Rundle, H. D. and Nosil, P. (2005) Ecological speciation. *Ecology Letters* **8**, 336–352.

Salzburger, W. and Meyer, A. (2004) The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. *Naturwissenschaften* **91**, 277–290.

Schluter, D. (2000) *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.

Seehausen, O. (2004) Hybridization and adaptive radiation. *Trends in Ecology and Evolution* **19**, 198–207.

Seehausen, O. (2006) African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society London B* **273**, 1987–1998.

Servedio, M. R. and Noor, M. A. F. (2003) The role of reinforcement in speciation: theory and data. *Annual Review of Ecology and Systematics* **34**, 339–364.

Simpson, G. G. (1953) *The Major Features of Evolution*. Columbia University Press, New York.

Spichtig, M. and Kawecki, T. (2004) The maintenance (or not) of polygenic variation by soft selection in heterogeneous environment. *American Naturalist* **164**, 70–84.

Streelman, J. T. and Danley, P. D. (2003) The stages of vertebrate evolutionary radiation. *Trends in Ecology and Evolution* **18**, 126–131.

Waxman, D. and Gavrilets, S. (2005) Issues of terminology, gradient dynamics, and the ease of sympatric speciation in Adaptive Dynamics. *Journal of Evolutionary Biology* **18**, 1214–1219.

Wu, C.-I. (2001) The genic view of the process of speciation. *Journal of Evolutionary Biology* **14**, 851–865.