

A New Mechanism for Recurrent Adaptive Radiations

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ABSTRACT: Models of adaptive radiation through intraspecific competition have attracted mounting attention. Here we show how extending such models in a simple manner, by including a quantitative trait under weak directional selection, naturally leads to rich macroevolutionary patterns involving recurrent adaptive radiations and extinctions. Extensive tests demonstrate the robustness of this finding to a wide range of variations in model assumptions. In particular, recurrent adaptive radiations and extinctions readily unfold both for asexual and for sexual populations. Since the mechanisms driving the investigated processes of endogenous diversification result from generic geometric features of the underlying fitness landscapes—frequency-dependent disruptive selection in one trait and weak directional selection in another—the reported phenomena can be expected to occur in a wide variety of eco-evolutionary settings.

Keywords: adaptive radiation, extinction, frequency-dependent selection, evolutionary branching, taxon cycle.

Changes in biodiversity result from speciation and extinction (McKinney and Drake 1998; Morris 1998) and may involve both endogenous and exogenous factors. Adaptive radiations driven by ecological interactions (Bush 1975; Schluter 1994, 2000; Feder et al. 1997; Grant 1998; Orr and Smith 1998) are key endogenous processes crucial for understanding the generation of biodiversity.

Theoretical studies have consistently emphasized the importance of frequency-dependent selection for driving

populations toward fitness minima at which selection turns disruptive and where adaptive radiations may thus occur (Rosenzweig 1978; Christiansen 1991; Brown and Pavlovic 1992; Metz et al. 1992, 1996; Abrams et al. 1993; Geritz et al. 1997, 1998; Cohen et al. 1999). Such processes have been termed “evolutionary branching,” and the locations of evolutionarily attracting fitness minima in an organism’s trait space are known as “evolutionary branching points.”

A plethora of studies have predicted evolutionary branching to occur in eco-evolutionary models of all fundamental types of ecological interaction (Doebeli and Dieckmann 2000). In particular, evolutionary branching has been studied in the context of symmetric intraspecific competition (Doebeli 1996*a*, 1996*b*; Metz et al. 1996; Dieckmann and Doebeli 1999), asymmetric intraspecific competition (Kisdi 1999; Doebeli and Dieckmann 2000; Kisdi et al. 2001), interspecific competition (Law et al. 1997; Kisdi and Geritz 2001), resource specialization (Meszéna et al. 1997; Geritz et al. 1998; Day 2000; Kisdi 2001; Schreiber and Tobiason 2003; Egas et al. 2004, 2005), ontogenetic niche shifts (Claessen and Dieckmann 2002), mixotrophy (Troost et al. 2005), phenotypic plasticity (Van Dooren and Leimar 2003; Ernande and Dieckmann 2004; Leimar 2005), dispersal evolution (Doebeli and Ruxton 1997; Johst et al. 1999; Parvinen 1999; Mathias et al. 2001; Parvinen and Egas 2004), mutualism (Doebeli and Dieckmann 2000; Law et al. 2001; Ferdy et al. 2002; Ferrière et al. 2002; Day and Young 2004), emergent cooperation (Doebeli et al. 2004), predator-prey interactions (Brown and Pavlovic 1992; Van der Laan and Hogeweg 1995; Doebeli and Dieckmann 2000; Bowers et al. 2003), cannibalism (Dercole 2003), host-parasite interactions (Boots and Haraguchi 1999; Koella and Doebeli 1999; Regoes et al. 2000; Gudelj et al. 2004), sex-ratio evolution (Metz et al. 1992; Reuter et al. 2004), evolution of selfing (Cheptou and Mathias 2001; De Jong and Geritz 2001), evolution of mating traits (Van Doorn et al. 2001, 2004), evolution of anisogamy (Maire et al. 2001), seed evolution (Geritz et al. 1999; Mathias and Kisdi 2002), microbial cross-feeding (Doebeli 2002), prebiotic evolution (Meszéna and Szathmáry 2001), resource competition among digital organisms (Chow et al. 2004), and evolutionary community

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assembly (Jansen and Mulder 1999; Bonsall et al. 2004; Loeuille and Loreau 2005). A recent review of findings in the related field of research on ecological character displacement (Brown and Wilson 1956) has been provided by Dayan and Simberloff (2005). The number of studies cited above indicates the extraordinarily wide range of ecological settings for which disruptive frequency-dependent selection may naturally cause evolutionary diversification. Addressing the origin, maintenance, and loss of biological diversity, analyses of these evolutionary processes contribute to an improved understanding of some of the most fundamental questions in biology.

To date, most studies of evolutionary branching have focused on a single quantitative character. Necessary and sufficient analytical conditions for evolutionary branching to occur in more than one-dimensional trait spaces have yet to be derived. Therefore, the question of how evolution in an extra quantitative character may interfere with processes of evolutionary branching has not been analyzed systematically yet. Here, we take a first step in this direction by considering the joint evolution of two quantitative characters, one of which is under frequency-dependent disruptive selection while the other is under weak directional selection. We explain how this simple extension of earlier models results in surprisingly rich macroevolutionary patterns involving recurrent adaptive radiations and extinctions. We find macroevolution in which evolutionary branching repeatedly occurs in the character under disruptive selection, with some of the resultant lineages subsequently being excluded by lineage-level selection on the character under directional selection, causing persistent Red Queen coevolution (Van Valen 1973) at the community level.

Complementing research into the ecological underpinnings of evolutionary diversification, another line of recent work has elucidated the circumstances under which the frequency-dependent disruptive selection pressures emerging at evolutionary branching points may overcome the genetic cohesion of sexually reproducing populations. Extending pioneering work by Maynard Smith (1966), Udovic (1980), and Felsenstein (1981), these studies have shown that, under some conditions, the degrees of reproductive isolation that can adaptively evolve at evolutionary branching points are sufficient even for sexual populations to split up under the pressure of disruptive selection (Dieckmann and Doebeli 1999; Kisdi and Geritz 1999; Kondrashov and Kondrashov 1999). In this way, sexual populations may escape from being perpetually trapped at fitness minima. How easily and quickly such escapes may be expected to occur is a matter of much current investigation and debate (e.g., Matessi et al. 2001; Bolnick 2004; Doebeli and Dieckmann 2005; Gavrillets 2005). Overviews are provided by Dieckmann et al. (2004) and Doebeli et

al. (2005). While our study here is primarily concerned with patterns of phenotypic evolution in asexual populations and therefore does not aspire to contribute to the more intricate controversies of contemporary speciation theory, an effort is nevertheless made to illustrate how our results about recurrent radiations and extinctions are expected to carry over to sexual populations.

This article is structured as follows. The section “Model Description” introduces models of bivariate evolution driven by intraspecific competition and details their individual-based foundation, both for asexual and for sexual populations. The section “Results” presents our main findings about the macroevolutionary patterns of recurrent radiations and extinctions resulting in these models. This is accompanied by a series of tests that critically evaluate the robustness of our findings. The section “Discussion” reflects on the generality of the evolutionary phenomena reported here and concludes with appraising their relevance for understanding taxon cycles.

Model Description

Real populations invariably evolve in multidimensional trait spaces. It must be assumed, therefore, that a population that reaches an evolutionary branching point in one trait will still experience directional selection in at least one other trait. In order to investigate the evolutionary implications of such presumably very common settings, we extend a standard family of models originally derived by MacArthur (1972) and used by Roughgarden (1974, 1976) to investigate the evolutionary consequences of intra- and interspecific competition.

One-Dimensional Model

Following many earlier studies, we consider individuals characterized by a one-dimensional quantitative character x that affects intraspecific competition (as, e.g., when beak size in birds determines the size of seeds they compete for). The per capita birth rate of individuals is assumed to be constant,

$$b(x) = r, \quad (1a)$$

while their per capita death rate, $d(x)$, depends on their trait value x as well as on abundances of extant phenotypes n_j for $j = 1, \dots, N$,

$$d(x) = r \sum_j \frac{\alpha(x_j - x)n_j}{K(x)}. \quad (1b)$$

Here,

$$K(x) = K_0 \exp\left[-\frac{x^2}{2\sigma_K^2}\right] \quad (1c)$$

is the carrying capacity of phenotype x , given by a Gaussian function with variance σ_K^2 peaked at 0. The function

$$\alpha(x_j - x) = \exp\left[-\frac{(x_j - x)^2}{2\sigma_\alpha^2}\right] \quad (1d)$$

describes the strength of competition between phenotype x and phenotype x_j ; it is also Gaussian with variance σ_α^2 and peaked at 0. Accordingly, the strength of competition is maximal between identical phenotypes and monotonically declines with phenotypic distance. In the limit of infinite population size, the assumptions above imply Lotka-Volterra population dynamics, $(d/dt)n_i = [b(x_i) - d(x_i)]n_i$ for $i = 1, \dots, N$. To scale time, we assume $r = 1$ without any loss of generality.

When the quantitative character x is allowed to adapt through rare and small steps $x \rightarrow x'$ from an initial value $x \neq 0$, the population first converges on the carrying capacity's maximum at $x = 0$. For $\sigma_\alpha > \sigma_K$, this outcome is evolutionarily stable. By contrast, when competition is sufficiently focused on similar phenotypes, $\sigma_\alpha < \sigma_K$, the population at the carrying capacity's maximum experiences a fitness minimum, resulting in disruptive frequency-dependent selection. In this situation, rare phenotypes $x \neq 0$ gain more from diminished competition with the common phenotype at $x = 0$ than they lose in terms of reduced carrying capacity. Accordingly, a gradually evolving monomorphic asexual population is expected to become dimorphic at the evolutionary branching point $x = 0$ (Metz et al. 1992, 1996; Geritz et al. 1997, 1998).

Model (1), or slight variants thereof, have been investigated by many authors, including Christiansen and Fenchel (1977), Christiansen and Loeschcke (1980), Slatkin (1980), Case (1981), Seger (1985), Taper and Case (1985), Vincent et al. (1993), Metz et al. (1996), Doebeli (1996a), Dieckmann and Doebeli (1999), Drossel and McKane (2000), Day (2000), Ackermann and Doebeli (2004), and Doebeli et al. (2007).

Two-Dimensional Model

Model (1) is readily extended to a two-dimensional quantitative character (x, y) ,

$$b(x, y) = r, \quad (2a)$$

$$d(x, y) = r \sum_j \frac{\alpha(x_j - x, y_j - y)n_j}{K(x, y)}, \quad (2b)$$

$$K(x, y) = K_0 \exp\left[-\frac{x^2}{2\sigma_{Kx}^2} - \frac{y^2}{2\sigma_{Ky}^2}\right], \quad (2c)$$

$$\alpha(x_j - x, y_j - y) = \exp\left[-\frac{(x_j - x)^2}{2\sigma_{\alpha x}^2} - \frac{(y_j - y)^2}{2\sigma_{\alpha y}^2}\right]. \quad (2d)$$

For any fixed y , $x = 0$ is an evolutionary branching point if $\sigma_{\alpha x} < \sigma_{Kx}$. However, Vukics et al. (2003) argued that evolutionary branching in this two-dimensional model only occurs at $(x, y) = (0, 0)$, since it is only at this point that directional selection pressures vanish for both x and y . This conclusion indeed holds when speeds of evolution in the two traits are comparable. In this case, two phenotypes forming a narrow dimorphism in trait x will typically be replaced by a mutant in trait y that is superior to both of them. If we assume, by contrast, significantly slower evolution in trait y than in trait x (resulting either from a weaker fitness gradient or from smaller or rarer mutations), the emergence of a dimorphism in trait x may lead to evolutionary diversification. As we will demonstrate in detail, in the section "Results," evolutionary branching may then also occur away from $(x, y) = (0, 0)$. The only requirement is that selection is frequency-dependent disruptive in one direction of trait space and weakly directional in the remaining direction. In the two-dimensional model (2), this situation arises for $\sigma_{\alpha x} < \sigma_{Kx}$ and $\sigma_{Kx} \ll \sigma_{Ky}$. Under these conditions, evolutionary branching may occur along the entire line $x = 0$.

Simplified Two-Dimensional Model

Directional selection on y can be due to any ecological interaction—including competition, predator-prey interaction, or mutualism—and can act on any morphological, physiological, life-history, or behavioral character y . A simple way of enhancing model (1) by introducing a fitness gradient in y is given by

$$b(x, y) = b(x) + b_1 \times (y - \bar{y}), \quad (3a)$$

$$d(x, y) = d(x) + d_1 \times (y - \bar{y}), \quad (3b)$$

where $b(x)$ and $d(x)$ are defined as in (1a) and (1b), \bar{y} denotes the population average of trait value y , $\bar{y} = \sum_j y_j n_j / \sum_j n_j$, and b_1 and d_1 are constants.

In this model, any shift in the distribution of y that changes \bar{y} but not the differences $y - \bar{y}$ leaves the popu-

lation's per capita birth and death rates unaffected, thus describing characters with demographic effects determined by relative trait differences rather than absolute trait values. This situation is typical for characters under frequency-dependent directional selection. Two key mechanisms implying such frequency dependence are trait-dependent density regulation and (conspicific or heterospecific) arms races. These may cancel the effects of directional evolution in a population's mean \bar{y} through density adjustments or concomitant evolution, respectively.

In model (3), composed of (3a) and (3b), the strength of directional selection in y , measured by the fitness gradient in y , is given by

$$G_y = \left. \frac{\partial[b(x, y) - d(x, y)]}{\partial y} \right|_{x=\bar{x}, y=\bar{y}} = b_1 - d_1. \quad (3c)$$

The strength of disruptive selection in x is measured by the second derivative of growth rate with respect to x . For a monomorphic population at $x = 0$, this yields

$$D_x = \left. \frac{\partial^2[b(x, y) - d(x, y)]}{\partial x^2} \right|_{x=\bar{x}=0, y=\bar{y}} = \sigma_\alpha^{-2} - \sigma_K^{-2}. \quad (3d)$$

Whenever $b(x, y)$ would become negative according to (3a), it is set to 0. When mutations are rare and small, $b(x, y)$ is almost always positive; rare mutations keep population dynamics close to the equilibrium at which $b(x, y)$ is close to $d(x, y) > 0$, and small mutations change these rates only slightly. Similarly, $d(x, y)$ in (3b) is set to 0 whenever it would become negative. How (3a) and (3b) can be derived from arbitrary forms of $b(x, y)$ and $d(x, y)$ is explained in appendix A.

As in the full two-dimensional model, evolutionary branching in the simplified model may occur along the line $x = 0$ when G_y is small compared with D_x . After such evolutionary branching, the resultant pair of lineages will continuously evolve in y under the constant directional selection pressure G_y . In the course of this evolution, which will usually be accompanied by further divergence in x , asymmetries in values of y naturally build up between the lineages, eventually destroying their coexistence. Thus, once evolutionary branching has occurred, extinction is inevitable. Our analyses below examine how this intricate interplay between radiations and extinctions unfolds.

Asexual Individual-Based Models

To allow for asexual evolution, we assume that with a small probability μ , a birth event involves a mutation. In the

one-dimensional model, mutant trait values x' are drawn from a univariate Gaussian distribution with variance σ_μ^2 , peaked at the parental phenotype x . In the two-dimensional models, mutant trait values (x', y') are drawn from a bivariate covariance-free Gaussian distribution with variances $\sigma_{\mu x}^2$ and $\sigma_{\mu y}^2$, peaked at the parental phenotype (x, y) .

The individual- and event-based asexual models defined by combining the mutation process specified above with the ecological rates specified for models (1)–(3) are implemented using Gillespie's minimal process method for homogeneous Markov processes in continuous time (Gillespie 1976; see also Dieckmann 1994; Dieckmann et al. 1995). Moreover, to enable the fast calculation of long-term evolutionary dynamics, asexual evolution is approximated by assuming low rates of mutation (our numerical analyses have confirmed that this approximation does not affect the dynamics in any qualitative way). Implementation details are provided in appendix B.

Sexual Individual-Based Models

Sexual evolution is incorporated into models (1) to (3) by considering male and female individuals, diploid inheritance, and quantitative characters coded for by multilocus genetics. There are various ways of modeling mating systems, including those directly based on ecological traits or, alternatively, on other mating traits. Since conditions for evolutionary branching have been shown to be more restrictive for the latter setting (Dieckmann and Doebeli 1999, 2004), we used a mating system based on additional mating characters, to check the robustness of results obtained for the asexual model under the most challenging conditions.

Specifically, L_x and L_y loci are considered for x and y , respectively, with integer allelic values and with the value of the coded quantitative characters being given by the average of allelic values across loci. To allow some flexibility with regard to recombination, C_x and C_y linkage clusters are considered for x and y ; while there is no recombination within such a cluster, recombination between them is free. Females produce offspring individuals at rate $2b_i$, where b_i denotes the per capita birth rate of a female i as specified by models (1)–(3). (The factor 2 arises in this correspondence since males do not bear offspring.) A female individual i chooses a male partner j for mating with probability

$$\tilde{P}_{ij} = \frac{P_{ij}b_j}{\sum_k P_{ik}b_k}, \quad (4a)$$

where b_j denotes the per capita birth rate of male j , and

the sum extends over all males in the population. The mating probability P_{ij} depends on a display character m_j in male j (e.g., pattern, color, song, dance, or gift) and on a corresponding preference character p_i in female i . These characters involve $L_m = L_p$ loci, which are organized into C_m and C_p linkage clusters. As for x and y , all allelic values are integers. The quantitative characters m_j and p_i are multivariate, with each of their components m_{i1}, \dots, m_{iL_m} and p_{i1}, \dots, p_{iL_p} being determined by averaging the two allelic values at the corresponding pair of homologous loci. The mating probability P_{ij} is then given by

$$P_{ij} = \exp \left[-\frac{d_{ij}^2}{2\sigma_m^2} \right], \quad (4b)$$

with

$$d_{ij}^2 = (p_i - m_j)^2 = \sum_{k=1}^{L_m} (p_{ik} - m_{jk})^2, \quad (4c)$$

so that d_{ij} measures the (Euclidian) distance between the preference of female i and the display of male j . Mating probabilities are thus increasing with the similarity between a male's display character and a female's preference character, with σ_m measuring the strength of female choosiness. Allelic mutations that increase or decrease allelic values (which happens with equal probability) occur with per locus probabilities of μ_x , μ_y , μ_m , and μ_p at the time offspring are formed. The sex of offspring is assigned at random, assuming an even primary sex ratio.

The individual- and event-based sexual models defined by combining the process of sexual reproduction specified above with the ecological rates specified for models (1)–(3) are again implemented using Gillespie's minimal process method. Implementation details are provided in appendix C.

Results

We first demonstrate the typical evolutionary dynamics of recurrent adaptive radiations and extinctions observed in the simplified two-dimensional model with asexual reproduction. We then show that the same dynamics arise in the full two-dimensional model and in models with sexual reproduction.

Recurrent Radiations and Extinctions

Our results reveal that the inclusion of directional selection in trait y qualitatively alters the observed macroevolutionary dynamics. Three different regimes can be distinguished.

First, in the complete absence of directional selection in trait y , $G_y = 0$, convergence to and evolutionary branching at $x = 0$ is followed by further processes of evolutionary branching, establishing a static configuration of lineages (fig. 1A). Owing to frequency-dependent selection, the current fitness landscape is contingent on the resident phenotypes. As long as the evolving resident population remains monomorphic, a single evolutionary branching point exists, $x_{b1} = 0$. Once the resident population has become dimorphic, this evolutionary branching point is replaced by two others, $x_{b2}^{(1)} = -x_{b2}^{(2)} \neq 0$, at which the resident population can become trimorphic and quadrumorphic. For finite populations, this process of sequential evolutionary branching results in no more than a finite number of lineages, because the residual strength of disruptive selection in trait x diminishes with each branching.

Second, when directional selection in trait y is very strong, evolution in trait y is so swift that it prevents diversification in trait x . After the population has converged to $x = 0$, it thus merely keeps evolving along this line in response to the directional selection pressure G_y (results not shown).

Third, when directional selection in trait y is finite and sufficiently weak, something very different happens: the initial branching in trait x is followed by a pattern of recurrent adaptive radiations and extinctions (fig. 1B). By comparing figure 1A and 1B, we can appreciate how the weak directional selection in trait y changes the macroevolutionary pattern. Instead of the static polymorphism resulting for the one-dimensional model—or, equivalently, for $G_y = 0$ —the two-dimensional model gives rise to incessant macroevolution, resulting in a more intricate, dynamically regenerating evolutionary tree.

The evolutionary mechanism responsible for the observed pattern of recurrent adaptive radiations and extinctions can be understood as follows. Right after evolutionary branching, stochastic effects—resulting from mutations as well as from the demography of finite populations—cause the spontaneous breaking of the initial symmetry between the two diverging lineages. In particular, the population sizes of the two lineages will never be exactly equal. Since the more abundant lineage can evolve faster, it will move ahead in the race of responding to the weak directional selection pressure in trait y , thus increasing its relative fitness in terms of trait y . We refer to the more abundant, leading lineage as the anterior lineage and to the less abundant, trailing lineage as the posterior lineage. The evolutionary interplay between these two lineages causes the asymmetry in their population sizes to grow and their trait values y to diverge. This positive feedback continues until the posterior lineage becomes extinct (fig. 1C). The positive feedback may be intensified by an

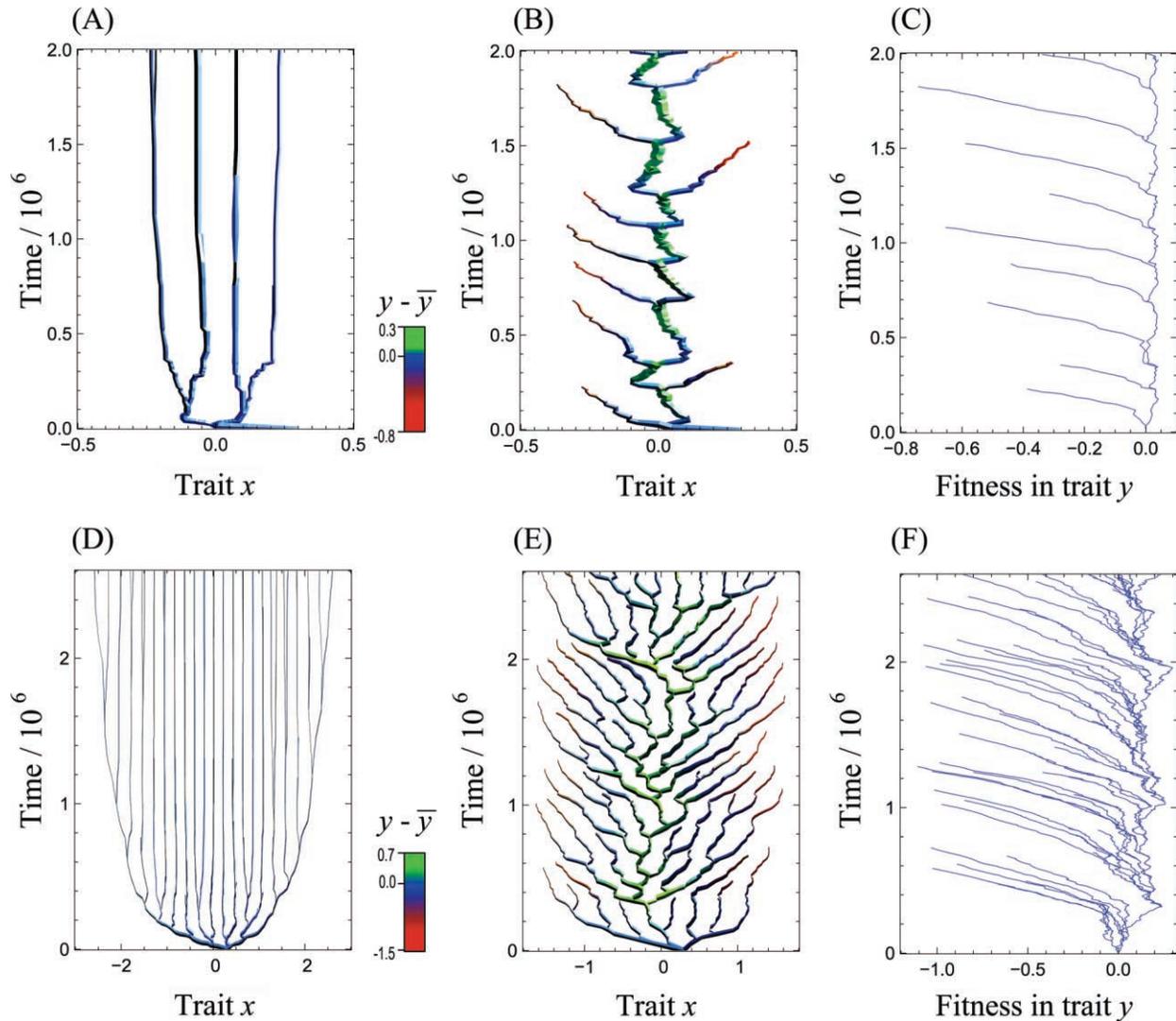


Figure 1: Evolutionary dynamics in the simplified two-dimensional asexual model. Upper panels (A–C) show the evolutionary dynamics for a medium width of the resource distribution in trait x ($\sigma_\kappa = 0.2$ compared with $\sigma_\alpha = 0.15$). A, No selection in trait y , $G_y = 0$. B, C, Weak directional selection in trait y , $G_y = 0.5$. Lower panels (D–E) show the evolutionary dynamics for a twice larger width of the resource distribution in trait x ($\sigma_\kappa = 0.2$ compared with $\sigma_\alpha = 0.07$). D, No selection in trait y , $G_y = 0$. E, F, Weak directional selection in trait y , $G_y = 0.5$. In panels A, B, D, and E, the widths of lineages indicate their population size with linear scaling, while the colors of lineages (green to blue to red) indicate their trait value y compared with the community's current average \bar{y} . In C and F, the horizontal axis shows $G_y(y - \bar{y})$, that is, the fitness component of lineages that derives from their trait y . Other parameters are $K_0 = 100,000$, $r = 1$, $\sigma_{\mu_x} = \sigma_{\mu_y} = 5 \times 10^{-3}$, $\mu = 10^{-5}$, and $\varepsilon = 1$.

additional effect: once the anterior lineage becomes sufficiently dominant, it experiences so little competition from the posterior lineage that it reverses its direction of gradual evolution in trait x , thus pushing the posterior lineage toward lower carrying capacity and accelerating its demise (fig. 1B).

Robustness

Niche Widths. We examined how these basic macroevolutionary patterns and mechanisms extend to ecological

settings involving broader fundamental niches. In our models, this corresponds to widening the carrying capacity function K with respect to trait x . Without directional selection in trait y , a large value of σ_κ (measured relative to the range of competition, σ_α) accelerates evolutionary branching and enables a larger number of coexisting lineages (fig. 1D). Similarly, when directional selection in trait y is weak but finite, a wide fundamental niche permits secondary and tertiary evolutionary branching before the first extinction occurs. This results in a larger number of

coexisting lineages becoming established and reestablished through the dynamic balance between adaptive radiation and extinction (fig. 1E).

While the evolutionary mechanisms underlying these patterns are the same as described above, the salient evolutionary interplay now occurs between several (instead of just two) lineages. Accordingly, we must interpret the macroevolutionary dynamics at the community level, in terms of anterior and posterior groups of lineages (fig. 1F). Yet another asymmetry-inducing evolutionary mechanism thus becomes important: anterior lineages are not only exhibiting faster gradual evolution but also faster adaptive radiations. This effect induces the explosive radiations of anterior lineages, accompanied by mass extinctions in all other lineages (see, e.g., the momentous radiation after $t = 0.3 \times 10^6$ in fig. 1E, 1F). When advantageous mutations in trait y are made large but rare, the described effect inevitably leads to evolutionary dynamics of the “punctuated equilibrium” type (Gould and Eldredge 1977).

Selection Strengths. How are these macroevolutionary patterns quantitatively affected by the strength of disruptive selection in x (measured by $D_x = \sigma_\alpha^{-2} - \sigma_\kappa^{-2}$) and by the strength of directional selection in y (measured by G_y)? In line with the qualitative results already described above, we find that adaptive radiations are inhibited when directional selection in y is too strong relative to disruptive selection in x (fig. 2). The corresponding critical relation between D_x and G_y roughly follows a linear relationship, $D_x \propto G_y$, in figure 2. Evolutionary community formation through adaptive radiations occurs for a wide range of selection strengths. Weaker directional selection in y and stronger disruptive selection in x both facilitate the build-up of larger communities (fig. 2), while stronger directional selection in y implies a more rapid turnover of species in the community.

Since the asexual individual-based model uses only the growth rate $b(x, y) - d(x, y)$ (app. B), different combinations of b_1 and d_1 sharing the same value of $b_1 - d_1$ (e.g., $d_1 = G_y$ and $b_1 = 0$) result in identical dynamics. More generally, recurrent radiations and extinctions are expected whenever (D_x, G_y) —the combination of the strength of disruptive selection in x and of directional selection in y —stays within the gray region in figure 2. Birth and death rates can thus depend on time or on other variables not considered here as long as (D_x, G_y) moves within the gray region. For example, replacing $G_y(y - \bar{y})$ with $G_y(y - y_0)$, using a constant y_0 or time-dependent variable $y_0 = a \times t$, can also induce recurrent radiations and extinctions.

Sexual Reproduction. Adaptive radiations in sexual populations require reproductive isolation. While our model

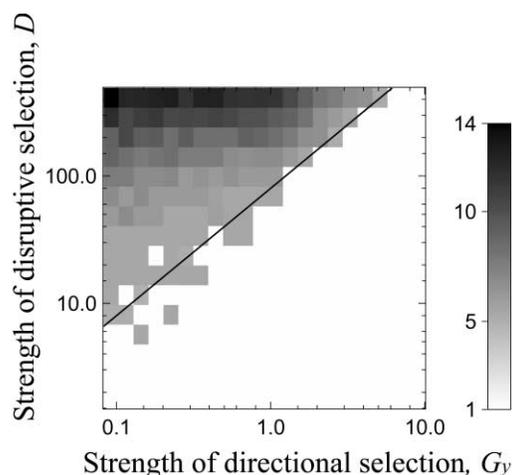


Figure 2: Number of coexisting lineages in the simplified two-dimensional asexual model. The number of lineages after 50,000 generations is shown for different strengths of directional selection, G_y , and for different strengths of disruptive selection, $D_x = \sigma_\alpha^{-2} - \sigma_\kappa^{-2}$. The continuous line shows the linear relationship $D_x = 80 \times G_y$. Other parameters are as in figure 1, except for $\sigma_{\mu x} = \sigma_{\mu y} = 2.5 \times 10^{-3}$.

with sexual reproduction is ecologically equivalent to the model with asexual reproduction analyzed so far, additionally, it allows for the emergence of prezygotic isolation through the divergence of male display and female preference traits.

Our results show that as expected from the asexual model, the sexual population first directionally evolves to $x = 0$. The disruptive frequency-dependent selection emerging at this evolutionary branching point then favors the pairwise divergence of male display trait m and female preference trait p (fig. 3A), triggered by small linkage disequilibria among x , m , and p (a similar effect was described by Dieckmann and Doebeli 1999). Subsequently, the divergence in mating traits m and p restricts interbreeding between the two lineages and enables their divergence in ecological traits x and y . Although disruptive selection weakens as interbreeding becomes rarer, divergence in m and p continues driven by genetic drift (Gavrilets 1997), leading to complete reproductive isolation (fig. 3A). This process of adaptive radiation accompanied by reproductive isolation occurs repeatedly, and the divergence among lineages in terms of trait y induces the extinction of posterior lineages (fig. 3B). The depicted macroevolutionary dynamics of ecological traits in the sexual model are thus equivalent to those observed in the asexual model.

Full Two-Dimensional Model. Macroevolutionary dynamics of repeated adaptive radiation and extinction also arise in the full two-dimensional model, both for asexual pop-

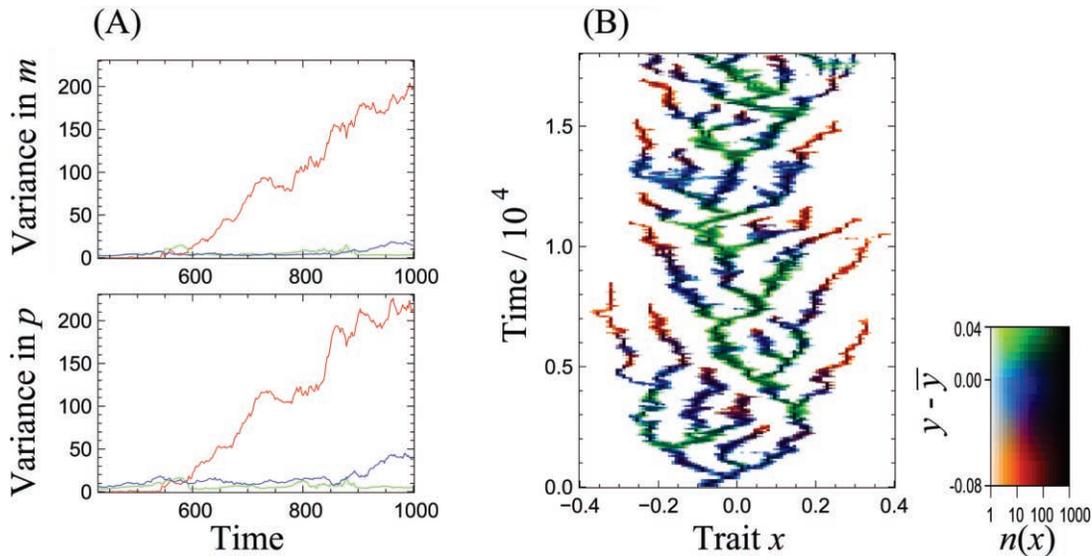


Figure 3: Evolutionary dynamics in the simplified two-dimensional sexual model. *A*, Evolution of reproductive isolation through divergence between male display trait (*upper panel*) and female preference trait (*lower panel*). The red curves show the variance between the two subpopulations, while the blue and green curves show the variances within each of these subpopulations. *B*, Evolution of the phenotype distribution. The rendering of pixels indicates the corresponding population size (*white to black*), as well as their average trait value \bar{y} (*green to blue to red*). At each moment, the subpopulations used in *A* are defined as falling on either side of a line drawn through the mean of the current phenotype distribution $n(x, y)$ and being orthogonal to this distribution's direction of maximum variance. Parameters: $K_0 = 500$, $\sigma_x = 0.2$, $\sigma_a = 0.07$, $r = 1$, $G_y = b_1 = 3.5$, $d_1 = 0$, $\sigma_m = 2.83$, $L_x = 60$, $L_y = 50$, $L_m = L_p = 20$, $\mu_x = 5 \times 10^{-5}$, $\mu_y = 10^{-5}$, $\mu_m = \mu_p = 5 \times 10^{-3}$, $C_x = 6$, $C_y = 5$, and $C_m = C_p = 2$.

ulations (fig. 4A) and for sexual populations (fig. 4B). While the rate of evolutionary change accelerates as the depicted dynamics approach the maximal carrying capacity, its other qualitative features are equivalent to those observed for the simplified two-dimensional model.

Mating Systems. For the sexual model discussed so far, we assumed that mating probabilities are determined by a male display trait and a female preference trait and that the birth rates of males and females together match those in the asexual model. However, large variations exist among the mating systems of organisms. For example, mating probabilities might depend on ecologically neutral traits expressed by males and females (mating variant 1) or on the ecological traits x and y (mating variant 2). These variants are especially important for describing ecological settings in which prezygotic isolation is brought about by habitat choice. Moreover, intrinsic rates of reproduction might not differ among males, so the effective reproduction rates of males might only depend on how often they are chosen by females (mating variant 3). Furthermore, the mating success, and thus the effective birth rate, of females preferring rare male display traits might be reduced, resulting in a cost of choosiness (mating variant 4).

We have checked the robustness of our results for sexual

populations against these variations of the mating system. Implementation details are provided in appendix D. Mating variants 1, 2, and 3 consistently result in recurrent adaptive radiations and extinctions. Mating variant 4 requires a sufficiently small cost of choosiness and sufficiently high mutation rates for the mating traits. A combination of mating variants 2 and 4 enables repeated radiations and extinctions also for larger costs of choosiness (app. D).

Spatial Structure. The requirements for recurrent adaptive radiations above are considerably relaxed when spatial structure is involved. We assumed that the carrying capacity's maximum gradually changes along a linear chain of patches connected by offspring migration. In each of these patches, birth and death events occur according to the simplified two-dimensional model as described above.

In such a parapatric setting, recurrent adaptive radiations and extinctions robustly occur under all four mating variants. In particular, for mating variant 4, they occur for larger costs of choosiness and/or for smaller mutation rates than in the corresponding nonspatial model if the migration probability is sufficiently low (app. E). This is just as expected, since the limited gene flow resulting from low migration rates favors the divergence of mating traits be-

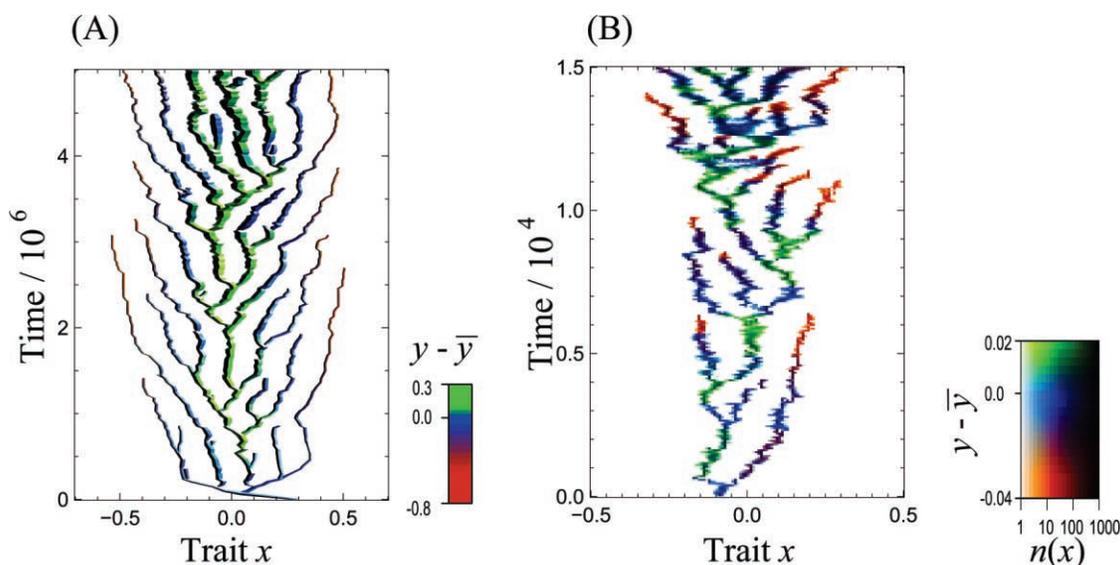


Figure 4: Evolutionary dynamics in the full two-dimensional model for (A) asexual reproduction and (B) sexual reproduction. The design of panels A and B matches that of figures 1E and 3B, respectively. Parameters for A: $K_0 = 100,000$, $\sigma_{Kx} = 0.2$, $\sigma_{Ky} = 0.5$, $\sigma_{ax} = 0.08$, $\sigma_{ay} = 0.6$, $\sigma_{\mu x} = \sigma_{\mu y} = 5 \times 10^{-3}$, and $\mu = 2.5 \times 10^{-5}$. The population in A is initialized at $y = -1.0$ and reaches a community average of $\bar{y} = -0.62$ at $t = 5 \times 10^6$. Parameters for B: $K_0 = 1,000$, $\sigma_{Kx} = 0.2$, $\sigma_{Ky} = 0.5$, $L_x = 60$, $L_y = 40$, $L_m = L_p = 20$, $\mu_x = 7 \times 10^{-5}$, $\mu_y = 10^{-6}$, and $\mu_m = \mu_p = 5 \times 10^{-3}$; other parameters as in figure 3. The population in B is initialized at $y = -1.0$ and reaches a community average of $\bar{y} = -0.28$ at $t = 1.2 \times 10^4$.

tween patches. Migration of phenotypes from an anterior lineage into patches with posterior lineages thus promotes the latter's extinction without interbreeding. We thus conclude that parapatric ecological settings further facilitate macroevolutionary processes of recurrent adaptive radiations and extinctions that, under more restrictive conditions, can already occur in sympatry.

Other Tests. In the simplified two-dimensional model with sexual reproduction, repeated adaptive radiations and extinctions were also observed for increased abundances (e.g., for total population sizes of around 3,000 individuals), smaller mutation probabilities of mating traits and higher choosiness (e.g., for $\mu_m = \mu_p = 10^{-4}$ and $\sigma_m = 2.0$), and smaller numbers of loci coding for each mating trait (e.g., for 10 loci). Although $d_1 = 0$ was used for figures 3 and 4, different combinations of b_1 and d_1 (including those with $b_1 = 0$) do not result in any qualitative change of the presented results. Other modifications, for example, replacing $b_1 \times (y - \bar{y})$ with $b_1 \times (y - y_0)$, using a constant y_0 or a time-dependent $y_0 = a \times t$, also induce recurrent radiation and extinction as long as D_x is sufficiently larger than G_y and a is small. Furthermore, we found that the explicit implementation of growth and aging of individuals did not qualitatively change the observed macroevolutionary dynamics.

Discussion

Evolutionary Branching in Multivariate Traits

The theory of adaptive dynamics has provided a general conceptual framework for understanding and analyzing the ecological conditions underlying processes of evolutionary diversification driven by ecological interactions (see Dieckmann et al. 2004 for an overview). However, most of the corresponding models (see the introduction to this article) are based on one-dimensional quantitative traits. In that case, adaptive radiations are expected to occur at evolutionary branching points, that is, at points in trait space where directional selection ceases and frequency-dependent disruptive selection remains (Metz et al. 1992, 1996; Geritz et al. 1997, 1998).

Under the assumption of infinitesimal mutation probabilities and mutational step sizes, the necessary conditions for evolutionary branching can be carried over from one-dimensional to higher-dimensional trait spaces; in particular, evolutionary branching will occur only where directional selection ceases in all directions. This would imply, however, that evolutionary branching in a focal trait cannot happen unless directional selection in all jointly evolving traits vanishes completely. Since all organisms possess more than a single evolving trait, that would make evolutionary branching all but impossible.

In reality, of course, mutation probabilities and muta-

tional step sizes may be small but are always finite. The results presented in this study illustrate that under these natural circumstances, evolutionary branching in multivariate quantitative traits may occur much more generally, whenever frequency-dependent disruptive selection in some trait directions is sufficiently strong compared with directional selection in the remaining trait directions. For understanding the occurrence of evolutionary branching in higher-dimensional trait spaces, traits that are under only weak directional selection can thus just as well be left out. This conclusion, however, does not extend to the eventual macroevolutionary patterns: when timescales are considered that are sufficiently long for such weakly selected traits to evolve significantly, they qualitatively affect the expected evolutionary outcomes. In particular, as shown above, recurrent adaptive radiations and extinctions can thus be induced.

It is interesting to note that the boundary in figure 2 implies a linear relationship between the strength of disruptive selection in x , D_x , and the strength of directional selection in y , G_y . Indeed, it can be shown analytically that for asexual populations, the likelihood of the first evolutionary branching is determined by $(\sigma_{\mu x}^2 D_x)/(\sigma_{\mu y} G_y)$, irrespective of the types of ecological interaction that influence birth and death rates (H. C. Ito and U. Dieckmann, unpublished manuscript).

Generality of Macroevolutionary Mechanism

The results presented here show how frequency-dependent disruptive selection in one trait combined with weak directional selection in another trait naturally and robustly lead to macroevolutionary patterns of recurrent adaptive radiations and extinctions. Such a combination of selection pressures must be expected to be common in nature. This is because frequency-dependent disruptive selection in univariate traits is predicted to occur under a wide variety of circumstances, in very different quantitative characters, and for many types of ecological interactions (see Doebeli and Dieckmann 2000 and references cited in the introduction to this article). Owing to the high dimensionality of real trait spaces and the ubiquity of externally driven changes in the ecological environments of organisms, some residual weak directional selection in at least one other trait direction can always be taken for granted. The requirements for inducing recurrent adaptive radiations and extinctions thus appear to be readily met in nature.

The evolutionary mechanisms underlying such incessant macroevolution are not difficult to understand and have been explained in detail in the section “Results”: while lineages best adapted to the directional selection pressures inevitably emerge through spontaneous symmetry breaking, they subsequently experience a positive feedback in

fitness that drives other lineages to extinction before the extinct lineages are replaced through adaptive radiations enabled by frequency-dependent disruptive selection. Macroevolutionary patterns broadly similar to those analyzed here have occurred repeatedly in evolutionary history. Examples include the radiation of angiosperms followed by the decline of gymnosperms (Wing and Boucher 1998) and the diversification of eutherian mammals replacing metatherian mammals (Lillegraven 1979).

Experimental tests of the macroevolutionary mechanism proposed here might be feasible in microbial organisms, in which adaptive radiations due to frequency-dependent selection have already been demonstrated (MacLean 2005). Including a second kind of trait and selection pressure—for example, by considering a character for temperature adaptation in addition to a character for resource competition—could immediately enable testing our predictions in real asexual populations.

Taxon Cycles

The results presented here have some bearing on the discussion of taxon cycles (Wilson 1961), which are based on likening the aging of species to that of individuals. In accordance with this perspective, we can indeed show that in our model the fitness component of lineages in the direction of directional selection monotonically decreases with a lineage’s age (fig. 5). This monotonicity underlies the “developmental cycle” of lineages and is caused by the positive feedback between a lineage’s fitness and its evolving position along the trait dimension subject to directional selection.

Cycles of evolutionary branching and extinction akin to taxon cycles had already been found in earlier theoretical studies (e.g., Taper and Case 1992; Kisdi et al. 2001). Such alternative models of taxon cycles, however, consistently had to rely on asymmetric ecological interactions. Here, we have shown that recurrent adaptive radiations and extinctions can occur even when all considered ecological interactions are strictly symmetric. In our model, asymmetry in the competition between lineages is of evolutionary rather than ecological origin and stems from a positive feedback mechanism that causes evolutionary divergence in a trait under weak directional selection.

The models presented here can also be employed to examine the lifetimes of lineages (fig. 5). Further work in this direction will help to complement other theoretical studies predicting lifetime distributions, including those based on self-organized criticality (Bak 1997; Pigolotti et al. 2005). We find that large values of D_x/G_y and G_y favor frequent radiations and extinctions, respectively. Such combinations are thus expected to shorten the lifetimes of lineages.

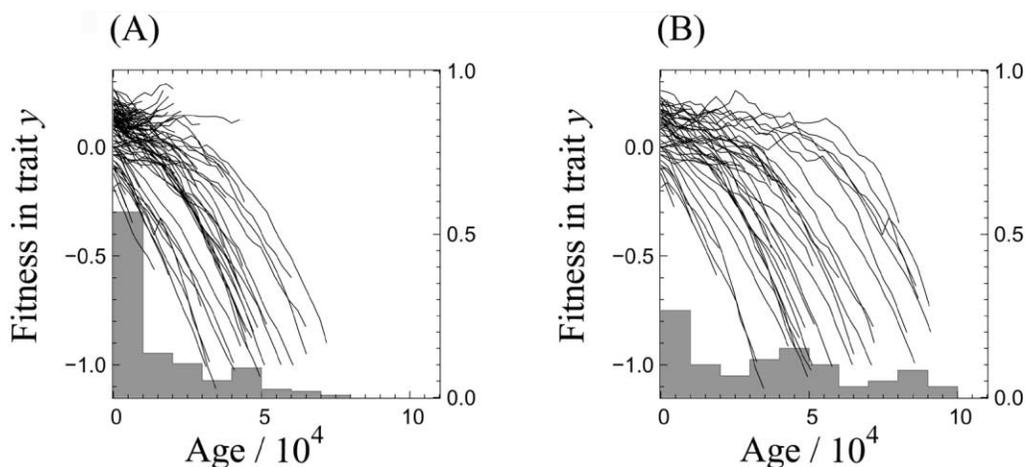


Figure 5: Relationship between the age of lineages and their fitness in trait y for the evolutionary dynamics shown in figure 1E. Ages of lineages are defined by assuming that at a branching of the evolutionary tree, (A) both lineages are assigned an age of 0 or (B) only one lineage, chosen at random, is assigned an age of 0, while the other lineage inherits its age from the common ancestor. The resultant distributions of lineage lifetimes are depicted at the bottom of each panel, with frequencies as indicated by the right vertical axes.

Summary

In this study, we have demonstrated how the straightforward extension of well-established univariate models of frequency-dependent disruptive selection, through the inclusion of a second trait under weak directional selection, induces recurrent adaptive radiations and extinctions, both in asexual and in sexual populations. That these macroevolutionary patterns can be understood in terms of general geometric features of bivariate frequency-dependent fitness landscapes explains their robustness. This means that the processes of recurrent adaptive radiations and extinctions reported here must be expected to occur even when the specific ecological underpinnings responsible for disruptive and directional selection pressures are altered. We thus hope that by offering an abstract and general framework with minimal ingredients, our model may serve as a stepping-stone for understanding macroevolutionary phenomena of wide-ranging relevance.

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APPENDIX A

Scope of Simplified Two-Dimensional Model

Models such as (3) are built on the simplifying assumption that the demographic effects of a population's distribution of character values can be captured through a character's average value. Models of this kind have been used extensively for studying the evolutionary ecology of frequency-dependent interactions (e.g., Abrams et al. 1993) and are known to approximate more general models when the considered character's variance is sufficiently small (Iwasa et al. 1991; Taper and Case 1992).

Applying this rationale to the character y in our two-dimensional model, we can express the frequency dependence in y of, for example, the population's per capita birth rate as $b(x, y, \bar{y})$. Here, the population's mean in the character y is $\bar{y} = \sum_j y_j n_j / \sum_j n_j$, and its variance in y , $\sigma_y^2 = \sum_j n_j (y_j - \bar{y})^2 / \sum_j n_j$, is assumed to be sufficiently

small. The first-order Taylor expansion of $b(x, y, \bar{y})$ in y around \bar{y} ,

$$b(x, y, \bar{y}) \approx b_0(x, \bar{y}) + b_1(x, \bar{y}) \times (y - \bar{y}),$$

will then be a good approximation, since differences $y - \bar{y}$ will be small.

To recover (3a), we thus need to assume that (a) the variance in the character y is not too large so that σ_y^2 is small (relative to the scale of potential nonlinearities in the dependence of b on y), (b) the baseline birth rate is determined by the character x so that $b_0(x, \bar{y}) = b(x)$, and (c) the sensitivity of b to variation of y around \bar{y} is constant so that $b_1(x, \bar{y}) = b_1$. The requirements for the per capita death rate d to be given by (3b) are analogous. The resultant set of assumptions thus delimits the conditions under which the simplified model (3) is applicable.

APPENDIX B

Asexual Model

To enhance the computational tractability of long-term asexual evolution driven by mutation and selection, we followed the usual assumption that evolutionary dynamics occur on a slower timescale than population dynamics. In the corresponding approximation (monomorphic stochastic model; Dieckmann 1994; Dieckmann et al. 1995; Dieckmann and Law 1996), mutations are rare so that evolution can be described as a directed random walk. In each step of this random walk, a mutant phenotype successfully replaces its ancestor. In the absence of evolutionary branching, invasion of a mutant phenotype generically implies replacement of the former resident phenotype (Geritz et al. 2002). Here we have extended this model to include evolutionary branching, resulting in what we call the oligomorphic stochastic model. The algorithm of the asexual model is listed below.

0. Initialize the phenotypes $s = (s_1, \dots, s_N)$ of all N resident lineages $k = 1, \dots, N$ at time $t = 0$ (an initial value of $N = 1$ is used throughout this study, corresponding to an initially monomorphic community). Calculate equilibrium population sizes $\hat{n} = (\hat{n}_1, \dots, \hat{n}_N)$ at which $b(s_k) = d(s_k)$ for all $k = 1, \dots, N$. Define the extinction threshold ε .

1. Calculate the rate $w_k = \mu \hat{n}_k b(s_k)$ for the emergence of a mutant from phenotype s_k as well as the total rate $w = \sum_{k=1}^N w_k$, where μ is the mutation rate.

2. Choose lineage i with probability w_i/w .

3. Choose a new phenotype s'_i according to the mutation probability density $\Omega(s'_i - s_i)$. Update time t by adding $\Delta t = -(1/w) \ln \rho$, where $0 < \rho \leq 1$ is a uniformly distributed random number. Calculate the invasion fitness $f(s'_i) = b(s'_i) - d(s'_i)$ of the new phenotype at \hat{n} .

4. Choose a uniformly distributed random number $0 < \rho \leq 1$. If $\rho \geq f(s'_i)/b(s'_i)$, return to step 2. Otherwise, calculate equilibrium population sizes $\hat{n}' = (\hat{n}'_1, \dots, \hat{n}'_p, \dots, \hat{n}'_N)$ for $s' = (s_1, \dots, s'_i, \dots, s_N)$.

5. If $\hat{n}'_k > \varepsilon$ for all $k = 1, \dots, N$ and $f(s'_i) < 0$ at \hat{n}' , replace s_i with s'_i and \hat{n} with \hat{n}' and continue with step 1. Otherwise, increase N by 1 and set $s_N = s'_i$. Calculate equilibrium population sizes from population dynamics with initial population sizes $n_k = \hat{n}_k$ for $k = 1, \dots, N - 1$ and $n_N = \varepsilon$. In the course of these population dynamics, delete phenotypes s_k with $\hat{n}_k < \varepsilon$ and decrease N accordingly. Continue with step 1.

APPENDIX C

Sexual Model

Sexual reproduction is implemented on an individual basis. The variables M_i and $F_i = 1 - M_i$ are used to indicate the sex of individual i : $M_i = 1$ if i is male, and $F_i = 1$ if i is female. The algorithm of the sexual model is listed below.

0. Initialize the genotypes and sexes of all N individuals $k = 1, \dots, N$ at time $t = 0$. Calculate the birth rates $b(s_k)$ and death rates $d(s_k)$ of all individuals $k = 1, \dots, N$.

1. Construct the sums $w_d = \sum_{k=1}^N d(s_k)$, $w_b = \sum_{k=1}^N 2b(s_k)F_k$, and $w = w_b + w_d$.

2. Choose a death or birth event with probabilities w_d/w and w_b/w , respectively. If a death event is chosen, continue with step 3; otherwise, continue with step 4.

3. Choose individual i with probability $d(s_i)/w_d$ and remove it from the population. Decrease total population size N by 1. Continue with step 5.

4. Choose female individual i with probability $2b(s_i)/w_b$. Construct the sum $w_M = \sum_{k=1}^N b(s_k)P_{ik}M_k$. Choose male individual j with probability $b(s_j)P_{ij}/w_M$. Assemble two haploid gametes through recombination from individuals i and j . Combine these gametes into the genotype of a diploid offspring and toggle alleles at each locus according to trait-specific mutation probabilities μ_x, μ_y, μ_m , and μ_p . Add a new individual with this genotype to the population and assign its sex at random. Increase total population size N by 1.

5. Update time t by adding $\Delta t = -(1/w) \ln \rho$, where $0 < \rho \leq 1$ is a uniformly distributed random number. Continue with step 1.

APPENDIX D

Mating Systems

We checked the robustness of our results against the following variations in the mating system:

Mating variant 1. Mating depends on ecologically neutral traits $q = (q_1, \dots, q_{L_q})$ expressed by males and females. Equation (4c) is replaced with $d_{ij}^2 = \sum_{k=1}^{L_q} (q_{ik} - q_{jk})^2$.

Mating variant 2. Mating depends on both ecological traits. Equation (4c) is replaced with $d_{ij}^2 = \beta^2[(x_i - x_j)^2 + (y_i - y_j)^2]$ (where $\beta = 10$ compensates for the difference in mutation probabilities of ecological traits and mating traits).

Mating variant 3. Intrinsic rates of reproduction do not differ among males. In step 4 of appendix C, a male individual j is chosen with probability P_{ij}/w_M , where $w_M = \sum_{k=1}^N P_{ik}M_k$.

Mating variant 4. Following Doebeli and Dieckmann (2003), a cost of choosiness is introduced. In steps 1 and 4 of appendix C, the intrinsic birth rate $2b(s_i)$ of female individuals is replaced with the effective birth rate $2b(s_i)/(1 + B_c/B_i)$, where $B_i = \sum_{j=1}^N b(s_j)P_{ij}M_j$ is the number of suitable mating partners. The parameter B_c measures the value of B_i at which the effective birth rate drops to half the intrinsic birth rate.

As described in the main text, recurrent radiation and extinction readily arises under mating variants 1 and 3 as well as under variant 2 if assortative mating is sufficiently strong (e.g., $\sigma_m = 5$). For variant 4 alone, small costs of choosiness are required (e.g., $B_c = 0.2$). A combination of mating variants 2 and 4 enables recurrent radiation and extinction at larger costs of choosiness (e.g., $B_c = 5$ for $\sigma_m = 5$).

APPENDIX E

Spatial Structure

We introduced spatial structure into the simplified two-dimensional model by considering a linear chain of N_z patches labeled $z = 1, \dots, N_z$. The carrying capacity distribution in the z th patch is given by

$$K(x, z) = K_0 \exp\left[-\frac{(x - zd_z)^2}{2\sigma_K^2}\right],$$

where d_z measures the difference between adjacent patches in the positions of the maximum carrying capacity. The abundance of extant phenotypes $j = 1, \dots, N$ in patch z is denoted by n_{jz} . The per capita birth and death rates of

individuals with characters (x, y) in the z th patch are given by

$$b(x, y, z) = r[1 + G_y(y - \bar{y}_z)],$$

$$d(x, y, z) = \frac{r \sum_j \alpha(x - x_j) n_{jz}}{K(x, z)},$$

where \bar{y}_z is the average value of y in the z th patch. Individuals mate within patches. Offspring migrate with probability ξ between adjacent patches.

Assuming sexual reproduction and mating variant 4, we could show that this spatial structure enables recurrent adaptive radiations even for large costs of choosiness and/or small mutation rates, if only the migration probability ξ is sufficiently low. For example, radiations occur for $B_c = 5$, $\mu_m = \mu_p = 5 \times 10^{-4}$, and $\xi = 5 \times 10^{-3}$, as well as for $B_c = 5$, $\mu_m = \mu_p = 5 \times 10^{-5}$, and $\xi = 5 \times 10^{-4}$. Other model parameters are $N_z = 3$, $d_z = 0.15$, $K_0 = 500$, $r = 1$, $\sigma_K = \sigma_\alpha = 0.14$, $G_y = 7.5$, $\sigma_m = 5$, $L_x = 40$, $L_y = 10$, $L_m = L_p = 15$, $\mu_x = 10^{-5}$, $\mu_y = 5 \times 10^{-6}$, $C_x = 4$, $C_y = 1$, and $C_m = C_p = 5$.

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