ADAPTIVE RADIATION DRIVEN BY THE INTERPLAY OF ECO-EVOLUTIONARY AND LANDSCAPE DYNAMICS

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We investigate an individual-based model of adaptive radiation based on the biogeographical changes of the Great African Lakes where cichlid fishes radiated. In our model, the landscape consists of a mosaic of three habitat types which may or may not be separated by geographic barriers. We study the effect of the alternation between allopatry and sympatry called landscape dynamics. We show that landscape dynamics can generate a significantly higher diversity than allopatric or sympatric speciation alone. Diversification is mainly due to the joint action of allopatric, ecological divergence, and of disruptive selection increasing assortative mating and allowing for the coexistence in sympatry of species following reinforcement or character displacement. Landscape dynamics possibly increase diversity at each landscape change. The characteristics of the radiation depend on the speed of landscape dynamics and of the number of geographically isolated regions at steady state. Under fast dynamics of a landscape with many fragments, the model predicts a high diversity, possibly subject to the temporary collapse of all species into a hybrid swarm. When fast landscape dynamics induce the recurrent fusion of several sites, diversity is moderate but very stable over time. Under slow landscape dynamics, diversification proceeds similarly, although at a slower pace.

KEY WORDS: Allopatric divergence, biogeography, character displacement, reinforcement, secondary contact, speciation.

Adaptive radiation is the rapid diversification of a single lineage into many species with a great diversity of ecological strategies (Simpson 1953; Schluter 2000; Rundell and Price 2009; Losos 2010). Although adaptive radiation is widely studied empirically, few theoretical investigations have explicitly treated it (Gavrilets and Losos 2009). Adaptive radiation is usually viewed as a generalization of the processes of speciation and adaptation to larger spatial and temporal scales (Gavrilets and Losos 2009). Although speciation and adaptation have been widely studied with mathe-

matical models and numerical simulations (Coyne and Orr 2004; Gavrilets 2004; Kawecki and Ebert 2004), such generalization is tricky, because adaptive radiation involves many factors (e.g., ecological, environmental, genetic, etc.) interacting in a complex way.

Several theoretical models for adaptive radiation explicitly investigate the emergence of many species in a fixed sympatric arrangement (van Doorn et al. 1998; Bolnick and Doebeli 2003; Chow et al. 2004; Ito and Dieckmann 2007; Melián et al. 2010). By contrast, the standard scenario of adaptive radiation—that is, repetitive allopatric speciation events and propagation of diversity by secondary contacts due to migration (Losos and Ricklefs 2009)—was explicitly modeled only by Gavrilets and Vose (2005,

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2009). Here, we build a model of adaptive radiation focusing on the case when secondary contacts result from biogeographical changes. Such processes, resulting in the repeated alternation of allopatry and sympatry, are called landscape dynamics (Keymer et al. 2000; Aguilée et al. 2009). They are thought to have contributed, for example, to the radiation of the cichlid fishes in the Great African Lakes (Sturmbauer 1998; Schwarzer et al. 2012).

The standard scenario of adaptive radiation (Gavrilets and Losos 2009; Losos and Ricklefs 2009) starts with multiple allopatric speciation events. Next, migration brings the different species into contact. Reinforcement may then act if reproductive isolation is not completed. In this scenario, ecological differentiation occurs either in allopatry (by adaptation to different conditions in different locations) or after migration (by character displacement). Repeated several times, these processes may generate an adaptive radiation. This is, for example, the accepted scenario for the radiation of Darwin's finches (Grant and Grant 1997), a scenario likely under a broad range of ecological and environmental conditions (Aguilée et al. 2011a). Importantly, this scenario of adaptive radiation is thought to require a great diversity of habitat types to generate a great diversity of species (Schluter 2000).

In an alternative scenario, secondary contacts are due to biogeographical changes. For example, fluctuations of water level due to climatic and geological changes are known to have spatially connected and disconnected different fish populations in the Great African Lakes (Owen et al. 1990; Galis and Metz 1998; Arnegard et al. 1999; Stiassny and Meyer 1999). The repetition of temporary spatial isolation and secondary contact generating and propagating new species, originally verbally described by Greenwood (1965), and termed the "species pump" by Terborgh (1992), may have significantly contributed to the radiation of the cichlid fishes in the Great African Lakes, especially in Lakes Malawi and Tanganyika (Sturmbauer 1998; Schwarzer et al. 2012). Several authors suggested that the species pump may also contribute to explain the diversity of vertebrate species, in particular among birds, in Amazonian forests (Haffer 1969; Terborgh 1992; Haffer 1997; Hill and Hill 2001; Sedano and Burns 2010). A migration event brings only one species into contact with another community. Conversely, a biogeographical change brings entire communities into contact. All species from formerly allopatric sites may then be subject to new ecological interactions. Each evolutionary process occurring at secondary contact may involve many species, and each species may be subject to several evolutionary processes such as reinforcement, character displacement or hybridization. The evolutionary outcome (i.e., success or failure of species coexistence) of such multispecies secondary contacts has not previously been addressed with theoretical models.

Biogeographical changes resulting in the repeated alternation of allopatry and sympatry may be common at different spatio-temporal scales. For example, the connections between populations may vary due to glaciations and postglacial secondary contacts (Hewitt 2000; Young et al. 2002; Zhang et al. 2008). Global climatic variations and geological processes may cause sea level changes, resulting in repetitive separations and fusions of islands (Cook 2008; Esselstyn et al. 2009). At a different scale, populations may oscillate between allopatry and sympatry due to the contemporary fragmentation and reconstruction of habitats because of human activities (Davies et al. 2006). Several authors have pointed out the necessity to take into account the likely shifts in the geographical arrangement during the speciation process (e.g., Schluter 2001; Rundle and Nosil 2005; Bolnick and Fitzpatrick 2007; Xie et al. 2007; Fitzpatrick et al. 2008; Johannesson 2010). The effect of such landscape dynamics has been studied in the simplified case of up to two sites and species (Aguilée et al. 2011b), but not yet in complex landscapes, potentially allowing for the emergence of multiple, interacting species.

In the present study, we investigate whether landscape dynamics may cause a radiation, and if so, by which evolutionary processes. We analyze a model with few habitat types, competition for resources generating disruptive selection on an ecological trait, and polygenic trait inheritance impeding sympatric speciation (Gavrilets 2003; Coyne and Orr 2004; Waxman and Gavrilets 2005). Under these assumptions, existing theory predicts radiations to be unlikely, at least not beyond one species per habitat type. Our model further assumes landscape dynamics mimicking those of the Great African Lakes (repeated fragmentation and fusion of lakes). We show that adaptive radiation may then be generated, disentangle the evolutionary mechanisms involved, and specify which type of landscape dynamics are most likely to generate a radiation.

Model and Methods

Our model is built upon five guiding assumptions. First, allopatric divergence is made possible by assuming that the landscape consists of a mosaic of three habitat types, each with a different ecological optimum, distributed among six sites. Second, sympatric speciation is made unlikely by assuming that phenotypic traits are determined by many independently segregating loci, with small effect of each allele on the trait value (Gavrilets 2003; Coyne and Orr 2004; Waxman and Gavrilets 2005). Third, the evolution of reproductive isolation is allowed via assortative mating based on similarity in ecological traits. Fourth, to allow the long-term coexistence of several species in sympatry, we use an ecological model based on Roughgarden's (1972) model which assumes a continuous distribution of resources. Fifth, the model includes landscape dynamics mimicking those of the Great African Lakes (repeated alternation of allopatry and sympatry).

Table 1. Notation and numerical values.

Evolving trait	Definition	
$z_i = (x_i, y_i)$	Individual i pair of ecological traits x_i, y_i	
a_i	Individual i choosiness trait	

Parameter	Definition	Default value
r	*Per-capita* birth rate	$r = 1$
K^*	Maximum of the carrying capacity function	$K^* = 400$
σ_K	SD of the carrying capacity function	$\sigma_K = 1$
$z^{*J} = (x^{*J}, y^{*J})$	Ecological optimum in a habitat J	$z^{*P} = (0, 0)$, $z^{*R} = (1, 0)$, $z^{*S} = (0, 1)$
σ_C	SD of the competition kernel	$\sigma_C = 0.5$
L_k	Number of diploid loci determining trait $k \in (x, y, a)$	$L_k = 16$
μ_k	Mutation rate at each locus of trait $k \in (x, y, a)$	$\mu_k = 10^{-3}$
s_k^2	Expected phenotypic variance of trait $k \in (x, y, a)$	$s_x^2 = s_y^2 = 0.0016$, $s_a^2 = 0.01$
n_s	Number of satellite sites	$n_s = 5$
f	Rate at which a border reappears	$10^{-3} \leq f \leq 10^{-2}$
c	Rate at which a border disappears	$10^{-5} \leq c \leq 10^{-3}$

ECOLOGICAL MODEL

This section describes the population dynamics and evolution in a focal, geographically isolated region. Dependence of the parameters upon landscape structure is detailed in section Landscape model.

Population dynamics and competition

We use a stochastic, individual-based version of the population growth and competition model of Roughgarden (1972) in a two-dimensional ecological trait space (Vukics et al. 2003). This model is analogous to the Lotka–Volterra competition model: population growth is logistic, and resource competition is density dependent. Competition is also assumed to be stronger between individuals with similar rather than dissimilar traits, naturally inducing frequency-dependent selection.

The population in the geographical region under consideration consists of $n(t)$ individuals at time t. Each individual i is characterized by a pair z_i of independently evolving ecological traits x_i and y_i determining its resource utilization strategy (see Table 1 for a summary of the notation). These traits could be, for example, for cichlid fishes, dental morphology and anatomical factors related to living at a certain depth, which are two traits on which depends their diet (Seehausen and Magalhaes 2010).

Individual i gives birth at constant rate r and dies at rate

$$d(z_i) = \frac{r}{K(z_i)} \sum_{j=1, j \neq i}^{n(t)} C(z_i - z_j), \qquad (1)$$

where K is the carrying capacity function and C is the competition function (see, e.g., Roughgarden 1972; Dieckmann and Doebeli 1999). The carrying capacity function implicitly models a continuous distribution of resources. It is unimodal bivariate Gaussian with maximum K^* at phenotype z^*, called the ecological optimum, and standard deviation σ_K:

$$K(z_i) = K^* \exp\left(-\frac{\|z_i - z^*\|^2}{2\sigma_K^2}\right), \qquad (2)$$

where $\|z_i - z^*\|^2 = (x_i - x^*)^2 + (y_i - y^*)^2$. Individuals i and j compete according to a unimodal Gaussian kernel $C(z_i - z_j)$ with standard deviation σ_C:

$$C(z_i - z_j) = \exp\left(-\frac{\|z_i - z_j\|^2}{2\sigma_C^2}\right).$$

All along this study, we assume $\sigma_C < \sigma_K$. Using a deterministic version of the above model (assuming a monomorphic, large population), Vukics et al. (2003) showed that when $\sigma_C < \sigma_K$, the population is predicted to evolve by directional selection to the ecological optimum z^* where it then experiences disruptive selection, that is, z^* is an evolutionary branching point (Geritz et al. 1998). In the case of cichlid fishes, disruptive selection on dental morphology and on anatomical factors related to living at a certain depth has been documented (Seehausen and Magalhaes 2010). Note that when $\sigma_C > \sigma_K$, z^* is a continuously stable strategy (Vukics et al. 2003): the population is expected to evolve to z^* where it then experiences stabilizing selection. This does not allow the long-term maintenance of several sympatric species (Aguilée et al. 2011b), and this is not considered here.

Reproductive isolation

We model reproductive isolation as in Aguilée et al. (2011b). Reproductive isolation follows from assortative mating based on similarity in ecological traits. Ecological traits are thus magic traits for speciation (Gavrilets 2004; Servedio et al. 2011). In the case of cichlid fishes, adaptation for feeding on a specific resource (dental morphology) and adaptations for living at a given depth were suggested to act as magic traits (Seehausen and Magalhaes 2010): individuals living at different depths do not meet, and thus do not mate, and similarly, individuals remain close to the resource they feed upon. Postzygotic reproductive isolation is not incorporated into the model.

We assume sexual reproduction, and that each individual i is characterized by an evolving choosiness trait a_i. At each birth event, the individual i chosen to reproduce randomly encounters a sexual partner j among the individuals of the opposite sex in

the same geographical region. The pair mates with probability $q(i, j)$, which depends on similarity in the ecological traits of the two partners (the cue and the preference trait are the ecological trait) and on choosiness of individual i:

$$q(i, j) = \begin{cases} \left(1 - \frac{1}{2}\exp\left(-a_i^2\right)\right)\exp\left(-\frac{\|z_i - z_j\|^2}{2u_i^2}\right) & \text{if } a_i > 0 \\ 0.5 & \text{if } a_i = 0 \\ 1 - \left(1 - \frac{1}{2}\exp\left(-a_i^2\right)\right)\exp\left(-\frac{\|z_i - z_j\|^2}{2u_i^2}\right) & \text{if } a_i < 0 \end{cases}$$

(3)

where $u_i = 1/(10a_i^2)$.

This Gaussian mating function has the minimal biological realism required: it is a continuous function in a_i, individual i has no preference when $a_i = 0$ and mates assortatively (resp. disassortatively) when $a_i > 0$ (resp. $a_i < 0$), and choosiness increases when $|a_i|$ increases. When individual i rejects partner j, another partner is randomly chosen and the process repeats until mating succeeds, or until individual i has rejected 50 potential partners. This represents a very small cost of choosiness (Schneider and Bürger 2006; Kopp and Hermisson 2008).

Genetic architecture and inheritance

The genetic architecture and inheritance rules are based on Claessen et al. (2008). Trait k ($k \in (x, y, a)$) is determined by L_k diploid, additive loci on autosomal chromosomes. We assume neither environmental effects, nor epistasis, nor dominance effects. Each allele can take any real value. The value of trait k is the mean of the $2L_k$ allele values determining this trait.

We assume independent segregation: at each locus, one offspring allele is randomly chosen from maternal and paternal alleles. Unless otherwise specified, we assume $L_k = 16$ so that each allele has a limited effect on the value of the phenotypic trait. Because of these assumptions, when selection is disruptive, sympatric diversification is severely delayed (Waxman and Gavrilets 2005; Claessen et al. 2007, 2008) and is expected to happen rarely on the time scales we investigate.

At birth, the offspring's sex is determined randomly assuming a balanced sex-ratio. Mutation occurs at each locus determining trait k with probability μ_k. The mutant allele value is drawn from a normal distribution with mean equal to the parental allele value and with standard deviation $s_k\sqrt{2L_k}$. This mutation size at the allele level results in a mutational variance s_k^2 at the level of trait k, regardless of the number of loci (van Doorn et al. 2004).

LANDSCAPE MODEL

The landscape structure and dynamics mimic, in a very simplified way, the ones of the Great African Lakes. The shoreline of Lakes Malawi and Tanganyika consists of two alternating major habitat types: rocky sites alternating with sandy sites (Danley and Kocher
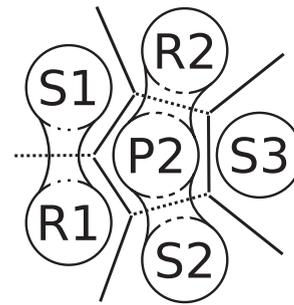
Figure 1. One possible state of the landscape with $n_s = 5$ satellite sites. Each circle depicts a site. The resource distribution of the central site defines it as a habitat P, satellite sites are habitats either R or S (indicated in circles). Each satellite site is possibly isolated by a border (solid segment) from the central site and from its neighboring satellite sites. The sites adjacent to a disappearing border (dotted segment) are fully connected (depicted by a "tunnel"). The number in each circle differentiates each isolated geographical region.

2001; Sturmbauer et al. 2011). Water level fluctuations induced the repetitive and temporary opportunity for individuals to freely move between neighboring sites (Owen et al. 1990; Galis and Metz 1998; Sturmbauer 1998; Arnegard et al. 1999; Stiassny and Meyer 1999).

We assume that the landscape consists of one central site surrounded by a ring of $n_s = 5$ satellite sites (Fig. 1). Each site is characterized by its resource distribution, defining a habitat type. We assume three different habitat types, labeled P, R, and S for pelagic zone, rocky habitat, and sand bottom. The resource distributions (eq. 2) have the same shape in all habitat types, that is, K^* and σ_K are independent of the habitat type, but they differ in their ecological optimum: $z^{*P} = (0, 0)$, $z^{*R} = (1, 0)$, and $z^{*S} = (0, 1)$. The central site is defined as a habitat P, and the habitat type of each satellite site is randomly chosen as either R or S at the beginning of each simulation run.

We assume that geographical barriers can isolate each site from neighboring sites (Fig. 1). Each border instantaneously disappears at rate c and re-appear at rate f. The sites adjacent to a disappearing border become fully connected (i.e., merged): individuals from the merged sites form a well-mixed population where all individuals compete and have access to all resources available in the merged sites. The carrying capacity function in merged sites is thus the sum of the carrying capacity functions of each of the constituting sites. Successive border disappearances can merge together multiple sites (up to $n_s + 1$ sites). Note that we do not consider here partial disappearances of a border (e.g., a small water level raise such that two close lakes become connected by a small river). The instantaneous fusion of sites into panmictic units is obviously a limiting case, but this is not expected to favor the occurrence of an adaptive radiation (see Discussion). When

an appearing border isolates two geographical regions, the individuals are distributed over the two isolated regions in proportion to the maximum carrying capacity of each region, independently of their phenotypes, that is, we assume no habitat selection at fragmentation events.

Given our choice of parameter values (Table 1), the carrying capacity function is unimodal whatever the number and the type of habitats of merged sites. There is thus always only one ecological optimum for any geographically isolated region, even if it consists of merged habitats of different types. For each possible combination of merged sites, we verified numerically that the ecological optimum is an evolutionary branching point (see section Population dynamics and competition) under the assumptions of a monomorphic, large population, and $\sigma_C < \sigma_K$ (not shown). We thus expect a single population in merged sites to evolve by directional selection to the ecological optimum and then to experience disruptive selection.

MODEL ANALYSIS METHODS

Our stochastic model is simulated using Gillespie's (1977) algorithm in continuous time. Results are computed over 50 simulation replicates running for 10^5 generations. The expected life span of an individual, which corresponds to one generation time, is one divided by the *per-capita* death rate. Details about the simulation procedure are in Appendix S1.
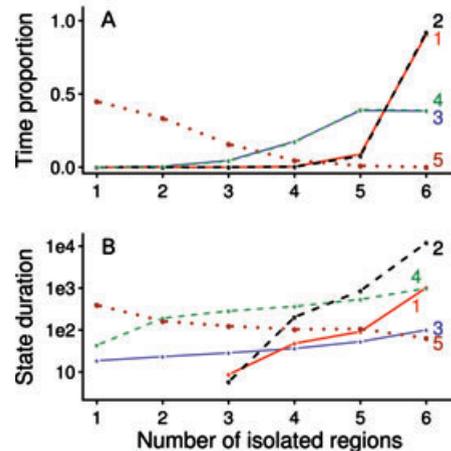
Types of landscape dynamics

Our model generates different kinds of landscape dynamics depending on the relative and absolute values of the rate at which each border appears (f) and disappears (c). Because each satellite site is surrounded by three borders, when $f > 3c$ (resp. $f < 3c$) sites are often isolated from each other (resp. merged with their neighboring sites). In addition, the higher f and c, the faster the dynamics. We analyze diversity generated by five types of landscape dynamics, simulated with the following sets of parameter values.

Case 1: Fast dynamics of a landscape with many fragments at steady state, simulated with $f = 10^{-2}$ and $c = 10^{-4}$. As $f \gg 3c$, the landscape is fragmented most of the time, and merged regions usually consist of no more than two sites (Fig. 2, panel A). The expected time spent in states with merged sites is less than 100 generations (Fig. 2, panel B), meaning that fusion of sites is rapidly followed by a new fragmentation.

Case 2: As case 1, but slow dynamics ($f = 10^{-3}, c = 10^{-5}$). Fusion is a rare event (Fig. 2, panel B): on average, more than 10,000 generations are spent in a completely fragmented landscape before a fusion occurs, and fragmentation occurs again after 1000 generations.

Case 3: Fast dynamics of a fragmented landscape with recurrently merged states ($f = 10^{-2}, c = 10^{-3}$). The landscape is

Figure 2. Characteristics of the landscape dynamics for different combinations of the parameters *f* and *c*, for a landscape with $n_s + 1 = 6$ sites. Panel A: proportion of the time during which the landscape is divided into a given number of geographically isolated regions, indicated on the *x*-axis. Panel B: mean duration (in generations, on a logarithmic scale) of time intervals during which the landscape consists of a given number of geographically isolated regions. The number next to each line indicates the type of dynamics, as defined in section Types of landscape dynamics (1: $f = 10^{-2}$, $c = 10^{-4}$; 2: $f = 10^{-3}$, $c = 10^{-5}$; 3: $f = 10^{-2}$, $c = 10^{-3}$; 4: $f = 10^{-3}$, $c = 10^{-4}$; 5: $f = 10^{-3}$, $c = 10^{-3}$). For cases 1 and 2, the landscape never consists of only 1 or 2 geographically isolated regions.

most of the time either completely fragmented or only two sites are merged, but a nonnegligible proportion of time is spent in states with more than two sites merged (Fig. 2, panel A). Each state duration is short (< 100 generations, Fig. 2, panel B): both fragmentation and fusion are frequent.

Case 4: As case 3, but slow dynamics ($f = 10^{-3}, c = 10^{-4}$). Each state lasts from 100 to 1000 generations (Fig. 2, panel B).

Case 5: Landscape with few fragments at steady state ($f = 10^{-3}, c = 10^{-3}$). Most sites are merged most of the time (Fig. 2, panel A). Each state lasts from 100 to 1000 generations (Fig. 2, panel B).

Diversity estimation

Our estimation of diversity is expressed as a number of species, in the sense of the biological species concept (Mayr 1942): two populations form distinct species when they are reproductively isolated, or would be if they were in sympatry. Diversity is computed by first grouping individuals into clusters of phenotypically close individuals, then evaluating the level of reproductive isolation between each pair of clusters. A continuous chain of clusters formed by pairs of reproductively non-isolated clusters defines a species (cohesion relaxed interpretation of the biological species concept, Gonzàlez-Forero 2009). This method, detailed in Appendix S2, is applied independently in each of the $n_s + 1$ sites of

the landscape to compute local (α) diversity. Total (γ) diversity is computed with the same method, but considering together all individuals of all sites.

Measures used in the Results section

We used three measures to characterize the diversity produced in a dynamic landscape: (1) the typical γ diversity which is the mean number of species after the initial diversification, (2) the time to reach typical γ diversity, and (3) the variance of typical γ diversity over time, which estimates the stability of γ diversity over time once typical γ diversity is reached.

We used two measures to interpret the above features of the diversity produced in a dynamic landscape. First, we compute allopatric divergence to measure how ecologically differentiated are the populations in geographically isolated regions with different ecological optima (i.e., allopatric populations which are expected to diverge). Allopatric divergence is computed as the ecological distance between pairs of geographically isolated populations, excluding pairs with the same ecological optimum. Second, we compute the minimal ecological distance between species from all sites combined (thus including both sympatric and allopatric species). When this distance is less than the minimal ecological distance between sympatric species only, which will always be true in our results, this distance is a minimal distance between species that are in allopatry. This minimal ecological distance between species from all sites combined thus allows us to evaluate the ecological nearness at which species can persist when they are in allopatry. We compute this measure as the ecological distance between the two phenotypically closest species, whether or not in allopatry once typical γ diversity is reached. These two measures are averaged over time.

These five quantities above are averaged over simulation replicates. The method used to compute them is detailed in Appendix S3.

Results

We first check the baseline behavior of the model by analyzing results in a static landscape. We show that the number of species generated in such a landscape does not exceed the number of habitat types. Then, these results are used as a benchmark to analyze the effect of landscape dynamics.

DIVERSITY IN A STATIC LANDSCAPE

According to Vukics et al. (2003), based on a model where sympatric diversification is unconstrained, up to approximately 10 ecologically differentiated species may coexist in an isolated site, assuming the parameter values in Table 1. In our model, however, we do not expect more than one species in each habitat, because sympatric speciation is impeded by strong genetic constraints.
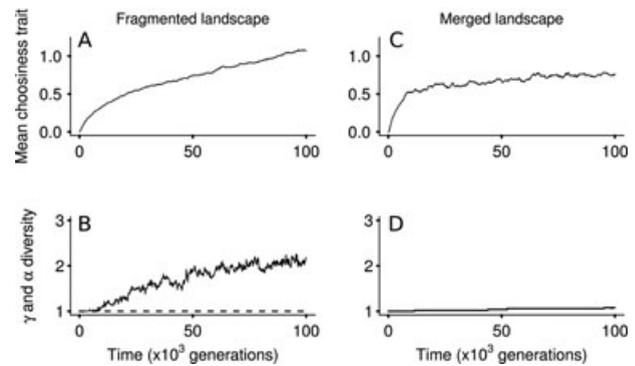
Figure 3. Diversity and mean choosiness trait in a static landscape. Panel A: time series of the mean choosiness trait in a fragmented, static landscape. Panel B: time series of γ (solid line) and α (dashed line) diversity in the same landscape. Panels C and D are replicates of, respectively, panels A and B, for a static landscape where all sites are merged together. For such a landscape, there is only one local population; α and γ diversities indicate the same quantity. Time series are averaged over simulation replicates. Parameter values: see Table 1. The equilibrium population size is about 400 individuals per site in a fragmented landscape, and about 2000 individuals in a landscape with all sites merged.

Consider a static landscape where all sites are permanently isolated. Allopatric populations in different habitat types diverge in their ecological traits and rapidly reach the local ecological optimum. Due to populations then experiencing disruptive selection, individuals become more choosy (a_i is positive and increases), that is, assortative mating based on similarity in the ecological traits increases (Fig. 3, panel A: increase of the choosiness trait averaged over individuals). After sometime, individual choosiness traits are on average high enough so that populations in different habitat types would, if in contact, so rarely produce hybrids that they can be considered as reproductively isolated. In brief, allopatric speciation occurs. Although disruptive selection at the ecological optimum tends to increase the genetic variance, genetic variance remains limited in each population. Because sympatric speciation is prevented by genetic constraints, assortment remains moderately strong (Fig. 3, panel A). This allows the maintenance of less genetic variation than under weak or strong assortment (Bürger and Schneider 2006; Bürger et al. 2006). Sympatric speciation is rare, so that local (α) diversity remains very close to one species (Fig. 3, panel B). As we assume three habitat types, we expect the emergence of three species at most. Total (γ) diversity, averaged over simulation replicates, remains below three (Fig. 3, panel B) because of stochastic reductions of assortative mating that temporarily break down reproductive isolation.

In a static landscape where all sites are permanently merged, assortative mating increases because of disruptive selection (Fig. 3, panel C), but allopatric divergence is obviously impossible. Diversity, averaged over simulation replicates, is
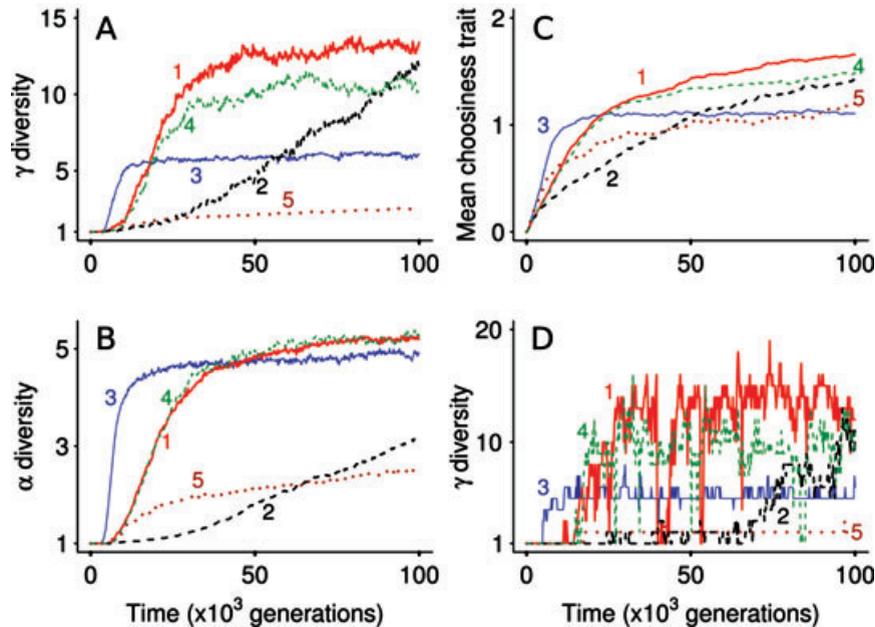
Figure 4. Diversity and mean choosiness trait in a dynamic landscape. Panels A–C show the time series averaged over simulation replicates of, respectively, γ diversity, α diversity, and the population mean choosiness trait. Panel D plots time series of one generic simulation replicate. The number next to each line indicates the type of dynamics, as defined in section Types of landscape dynamics. Parameter values: see Table 1. The total population size varies from about 2000 to 8000 individuals, depending of the number of species. Table 2 gives the values of some characteristics of γ diversity shown in panel A.

nevertheless slightly higher than one (Fig. 3, panel D) due to occasional sympatric speciation events.

DIVERSITY IN A DYNAMIC LANDSCAPE

Compared to a static landscape, a dynamic landscape clearly produces a large total diversity: up to 12.88 species on average (Fig. 4, panel A), and up to 24 species in individual simulation replicates; γ diversity is thus much higher than the number of habitat types. In each habitat, the ecological space may support up to approximately 10 ecologically differentiated species, but their emergence may be a limiting process. Landscape dynamics allow the emergence of a local diversity of five different species on average (Fig. 4, panel B), and up to 11 species in individual simulation replicates. The mechanism producing diversity in a dynamic landscape is analogous to the species pump (Greenwood 1965; Terborgh 1992).
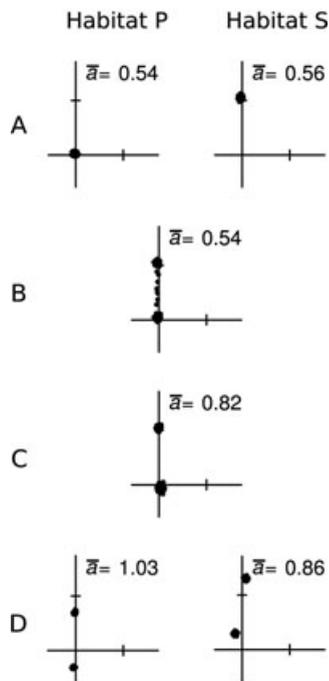
The allo-sympatric radiation process: the species pump

Consider first a simplified landscape with two sites holding two different habitat types. When the landscape is fragmented, allopatric populations in the two habitat types diverge as they adapt to the local ecological optimum (Fig. 5, panel A). Next, due to disruptive selection, assortative mating increases (Fig. 5, panel A). At secondary contact, the two former allopatric populations may be sufficiently reproductively isolated and ecologically differentiated to stably coexist (allopatric speciation). When the populations are

imperfectly reproductively isolated, reinforcement increasing assortative mating may complete speciation (Fig. 5, panels B and C). Alternatively, when they are weakly ecologically differentiated, character displacement may occur, reducing competition between species and allowing their stable coexistence. When the two sites become geographically isolated again, the two species coexist in each of the two isolated sites. The two pairs of species then diverge as they adapt to their local ecological optimum (Fig. 5, panel D). In each site, no species sits at the local ecological optimum: species sit symmetrically to the optimum. The four species present after the second allopatric divergence phase are thus different from the two species present after the first allopatric divergence phase.

Each time this sequence of secondary contact and fragmentation is repeated, local diversity may be propagated to other sites, and new species may be generated and maintained by first allopatric divergence, then reinforcement or character displacement. Diversity may thus increase at each landscape change.
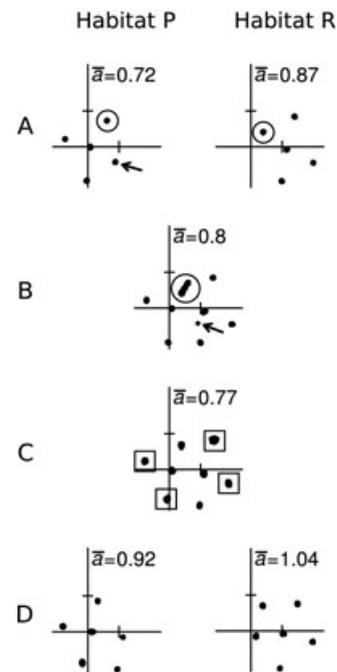
Figure 4 (panels A and B) shows that γ and α diversities saturate (except under landscape dynamics of type 2, as defined in section Types of landscape dynamics: this will be discussed later). When the whole ecological space is filled with species, the species pump may stop because of the following reasons, illustrated by Figure 6. First, reinforcement may fail at secondary contact, resulting in the fusion of two populations into a phenotypically intermediate hybrid population (circled populations in Fig. 6, panels A and B). Second, character displacement may fail

Figure 5. The allo-sympatric radiation process: the species pump. Each graph corresponds to a geographically isolated region and depicts by a dot an individual in the ecological trait space (*x*, *y*). The type of habitat in isolated regions is indicated on top of each panel. The tick on the *x*-axis (resp. *y*-axis) indicates the ecological optimum in a habitat R (resp. S); the ecological optimum of a habitat P is at the crossing of the two axes. The mean choosiness trait *ā* of the population in each isolated region is indicated on each graph. Panel A: state of the population one generation before the fusion of the two isolated regions depicted. Panel B: five generations after fusion. Panel C: 4000 generations after fusion, corresponding to one generation before fragmentation of the landscape; fragmentation results in the same landscape structure as depicted on panel A. Panel D: 10,000 generations after fragmentation. Parameter values: see Table 1. Total population size is about 1200 individuals.

Figure 6. Three reasons why the species pump may fail. Each graph depicts the population state as in Figure 5. Circles show species hybridizing at secondary contact. Arrows indicate species going extinct by competitive exclusion at secondary contact. Squares show species going extinct locally because of maladaptation after fragmentation of the landscape. Panel A: one generation before fusion. Panel B: 22 generations after fusion. Panel C: 1000 generations after fusion, one generation before fragmentation. Panel D: 2000 generations after fragmentation. Parameter values: see Table 1. Total population size is about 2000 individuals.

at secondary contact, so that ecologically close species go extinct due to competitive exclusion (species indicated by an arrow in Fig. 6, panels A and B). Third, when two merged sites holding different habitat types split, one of the two habitat types is no longer available in each isolated site. Species that are farther from the local ecological optimum suffer from maladaptation and may go extinct (squared species in Fig. 6, panel C).

Assortative mating increases due to disruptive selection in both static and dynamic landscapes, but only in dynamic landscapes does assortative mating possibly increase due to reinforcement at secondary contact. Therefore, the mean choosiness trait increases to higher values in dynamic landscapes than in static landscapes (Fig. 4, panel C vs. Fig. 3, panels A and C).

Case 1: Fast dynamics of a landscape with many fragments at steady state

Table 2 shows that the highest typical γ diversity is generated by fast dynamics of a landscape with many fragments at steady state. Two reasons explain this result.

First, the species pump very efficiently generates and maintains diversity. Because the landscape is mainly fragmented, populations in different habitat types often remain in allopatry long enough to widely diverge (Table 3) and to reach their evolutionary steady state where assortative mating increases. At secondary contact, populations are likely to be sufficiently ecologically differentiated and reproductively isolated to stably coexist (or for reinforcement and character displacement to be successful).

Second, the set of local species can be different in each site, even in sites holding the same habitat type, which results in γ diversity significantly higher than α diversity (Fig. 4, panel A vs. panel B). In sites holding the same habitat type, species are expected to be ecologically very similar. Such species can nevertheless be different, because (1) the arrangement of species may rotate around the ecological optimum, and (2) demographic stochasticity

Table 2. Characteristics of γ diversity in a dynamic landscape. The cases of landscape dynamics are those defined in section Types of landscape dynamics. The method used to compute the characteristics of γ diversity shown in this table is explained in section Measures used in the Results section. The symbol ± is followed by the SD among simulation replicates of each estimation. The time to reach typical γ diversity is indicated in thousands of generations. Under landscape dynamics of type 2, the typical γ diversity is not yet reached when simulations end, that is, after 10^5 generations (Fig. 4, panel A); the typical γ diversity and its variance over time are thus not available.

Case of landscape dynamics	Typical γ diversity	Time to reach typical γ diversity	Variance of typical γ diversity over time
1	12.88±2.22	30.13±9.17	5.71±3.49
2	–	> 100	–
3	5.99±0.99	13.91±8.84	0.46±0.42
4	10.59±1.66	28.87±10.97	4.01±2.43
5	2.34±0.81	32.58±23.69	0.03±0.05

may lead to small variations of phenotypic traits around their equilibrium values. In addition, because allopatric species do not suffer from competitive exclusion, such species can persist in allopatry despite being ecologically very close. Table 3 shows this ecological nearness by indicating that the minimal ecological distance between species from all sites combined is significantly less than the minimal ecological distance between sympatric species only: there exist thus allopatric species ecologically much more similar than sympatric species are.

Table 2 shows that the variance of the typical γ diversity over time is the highest under landscape dynamics of type 1. Total diversity can indeed temporarily collapse, as this happens in the simulation shown in Figure 4 (panel D). Such collapse is due to the fusion of possibly all species into a hybrid swarm, as illustrated by Figure 7. Under landscape dynamics of type 1, ecologically very close species exist in allopatry (Fig. 7, panel A). Such species cannot coexist in sympatry due to limiting similarity. At secondary contact of such species, either ecological differentiation increases, or species become extinct, or reproductive isolation breaks down. In the latter case, two populations ecologically very close begin to hybridize, which increases their phenotypic variance. This decreases the ecological differentiation between them and their ecological neighbors, allowing hybridization with their ecological neighbors also, and possibly generating a hybrid swarm rapidly spreading to the whole ecological space (Fig. 7, panels B and C). Assortative mating may then decrease, because the generation of many hybrids weakens the efficiency of selection against less choosy individuals. The huge genetic variance in the population then facilitates sympatric speciation,

Table 3. Allopatric divergence and minimal ecological distance between species in a dynamic landscape. The cases of landscape dynamics are those defined in section Types of landscape dynamics. The method used to compute the measures shown in this table is explained in section Measures used in the Results section. The symbol ± is followed by the SD among simulation replicates of each estimation. The values of allopatric divergence are to compare to 0.85 ± 0.10 which is the allopatric divergence measured in a fragmented, static landscape (computed from simulations of Fig. 3), that is, the maximum of allopatric divergence under the assumptions of our model. The values of the minimal ecological distance between all species (i.e., from all sites combined) are to compare to the minimal ecological distance between sympatric species of the same landscape dynamics type. The latter indeed depends on the level of assortative mating, which differs between the landscape dynamics types (Fig. 4, panel C). The minimal ecological distances are computed after γ diversity reaches its typical level; under landscape dynamics of type 2, the typical level of γ diversity is not yet reached at the end of simulations (Fig. 4, panel A), so that the minimal ecological distance is not available.

Case of landscape dynamics	Allopatric divergence (maximum: 0.85±0.10)	Minimal ecological distance between all species	Minimal ecological distance between sympatric species
1	0.67±0.13	0.16±0.04	0.68±0.03
2	0.77±0.14	–	–
3	0.52±0.12	0.81±0.07	0.88±0.04
4	0.62±0.12	0.31±0.09	0.74±0.03
5	0.25±0.07	0.86±0.27	0.98±0.10

which may occur, regenerating some diversity (Fig. 7, panel D). This can however take long to happen: before that, the hybrid swarm may propagate to all other sites by secondary contacts, destroying all diversity in the landscape. Note the high standard deviation among simulation replicates of the variance of typical γ diversity over time (Table 2) indicating that diversity collapse does not occur consistently.

Case 2: Slow dynamics of a landscape with many fragments at steady state

Here, the landscape is mainly fragmented and diversification is achieved in the same way as in case 1. Allopatric populations widely diverge (Table 3) and reach their evolutionary steady state where assortative mating increases. However, in case 2, secondary contacts are rare because the landscape dynamics are slow. Local diversity is thus rarely propagated to other sites, so that the time to reach typical γ diversity is very long (higher than 10^5 generations, Fig. 4, panel A). Assortative mating increases more slowly under slow than under fast landscape dynamics (Fig. 4, panel C) since
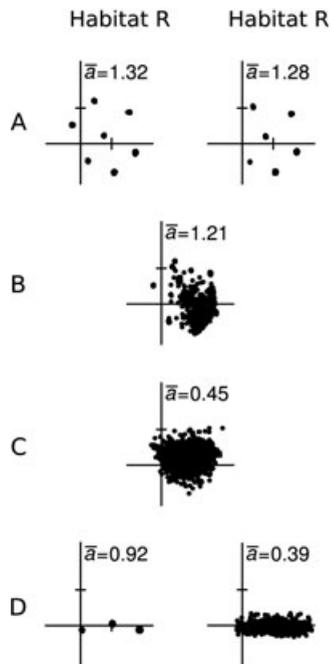
Figure 7. Secondary contact resulting in the fusion of all species into a hybrid swarm. Each graph depicts the population state as in Figure 5. Panel A: one generation before fusion. Panel B: 10 generations after fusion. Panel C: 1000 generations after fusion, one generation before fragmentation. Panel D: 5000 generations after fragmentation. Parameter values: see Table 1. Total population size is about 1800 individuals.

secondary contacts, and thus possible reinforcement events, occur less frequently.

Case 3: Fast dynamics of a fragmented landscape with recurrently merged states

In case 3, γ diversity is higher than in a static landscape, but remains moderate, hardly higher than α diversity (Fig. 4, panels A and B). The sets of local species are indeed often the same in all sites, even in sites holding different habitat types, because of frequent fusions of sites having the following consequences.

First, fusions of sites often occur before allopatric populations have ecologically widely diverged. Although allopatric divergence reaches high enough values for the species pump to produce diversity, allopatric divergence remains on average moderate (Table 3). The sets of local species in geographically isolated regions with different habitat types are thus likely to be ecologically close, and therefore to hybridize at secondary contact. The hybrid population may then replace the incipient species, destroying the onset of divergence.

Second, ecologically very similar allopatric populations may be very choosy so that they do not hybridize at secondary contact. Such species do however not survive for a long time: fusions of sites bring them into contact quickly after their emergence, and

competitive exclusion prevents their stable coexistence. Consequently, fast landscape dynamics with recurrently merged states maintain a high minimal ecological differentiation between all species, close to the minimal ecological distance between sympatric species (Table 3).

Thanks to this high differentiation between all species, the collapse of diversity because of the fusion of all species into a hybrid swarm is unlikely: the low variance of the typical γ diversity over time (Table 2), demonstrates that γ diversity remains very stable over time. This stability is illustrated by a typical time series shown in Figure 4 (panel D).

Typical γ diversity is reached very quickly (Table 2). Fusions of sites often occur and involve many sites, so that as soon as diversity is generated in allopatry, it is propagated to other sites, possibly several sites at the same time, which speeds up diversification. The standard deviation among simulation replicates of the time to reach typical γ diversity is however high compared to its average (Table 2), because allopatric divergence is on average moderate (Table 3). Because secondary contacts are frequent, reinforcement is common, and assortative mating increases very quickly (Fig. 4, panel C).

Case 4: Slow dynamics of a fragmented landscape with recurrently merged states

When the landscape is fragmented with recurrently merged states, the increase in diversity is slower under slow dynamics than under fast dynamics (Table 2: case 4 vs. case 3). Local diversity is indeed propagated by secondary contacts, which are less frequent under slow landscape dynamics.

Compared to case 3, allopatric states last longer in case 4, so that allopatric divergence is wider (Table 3), and geographically isolated regions are more likely to hold ecologically close species (Table 3: the minimal ecological distance between all species is significantly lower than that between sympatric species). Consequently, geographically isolated regions more often hold different sets of local species, resulting in a higher typical γ diversity (Table 2).

The flip side of this low ecological differentiation between all species is a weak stability of the typical γ diversity (Table 2: high variance of typical γ diversity over time). Hybrid swarms are likely to be generated at secondary contact, destroying diversity, as this happens in the time series shown in Figure 4 (panel D). However, diversity collapse does not occur in all simulation replicates (Table 2: high standard deviation among simulation replicates of the variance of γ diversity over time).

Case 5: Landscape with few fragments at steady state

No radiation is generated in a landscape with few fragments at steady state: the typical γ diversity does not exceed that of a static landscape (Table 2). Because most sites are most of the time

merged together, allopatric divergence is weak (Table 3), so that the generation of new species is rare. As species are most of the time in sympatry, α diversity is almost equal to γ diversity (Fig. 4, panel A vs. panel B), and all species are highly ecologically differentiated (Table 3).

Discussion
MAIN FINDINGS AND IMPLICATIONS

We analyzed a model with three habitat types, thus offering few opportunities for allopatric divergence, and with polygenic trait inheritance impeding sympatric speciation. Under these assumptions, a static landscape with no migration generates very little diversity: one species per habitat at most. We showed that, by contrast, landscape dynamics (repeated alternation of allopatry and sympatry) can generate a radiation, with significantly more species than the number of habitat types. During such a radiation, diversity is generated by the joint action of allopatric, ecological divergence under directional selection toward different ecological optima, and of disruptive selection favoring the evolution of assortative mating based on similarity in ecological traits.

Populations become reproductively isolated when ecological differentiation and assortative mating are both high enough (recall that we consider prezygotic reproductive isolation only). Reproductive isolation is often imperfect at secondary contact: disruptive selection then leads to reinforcement and character displacement, which completes speciation. Landscape dynamics constantly alter the (co)existing species, by a complex combination of hybridization, occasional sympatric diversification and frequent extinctions by competitive exclusion or local maladaptation. This results in different conditions at each secondary contact: although secondary contact always occurs between the same three habitat types, its outcome (success or failure of species coexistence) possibly changes at each new contact. Consequently, after several secondary contacts, the conditions necessary to reach each part of the ecological space are likely to have been fulfilled.

The characteristics of the diversity produced in a dynamic landscape are strongly correlated to the characteristic time scales of the landscape dynamics (Fig. 4, Table 2). In particular, the highest typical diversity is generated by fast dynamics of a landscape with many fragments at steady state, but diversity is then unstable: because of the ecological nearness of many species, diversity is likely to collapse into a hybrid swarm, then to be regenerated mainly by sympatric speciation. According to Seehausen (2004) and Schwarzer et al. (2012), such a mechanism may have had a great influence in the radiation of cichlid fishes, and possibly in other radiations (e.g., Darwin's finches, Hawaiian fruit flies or Hawaiian crickets; see also the model of Gilman and Behm 2011). Surprisingly, a similar pattern of radiation is generated by slow dynamics of a fragmented landscape with recurrently

merged states. Diversity is generated the fastest under fast dynamics of a fragmented landscape with recurrently merged sites, which indeed allow the rapid propagation of diversity to the whole metapopulation. Under such type of landscape dynamics, diversity remains stable, but moderate. Finally, dynamics of a rarely fragmented landscape generate little diversity (no radiation).

Mathematical and computational models of speciation usually focus on one specific geographical background (but see Aguilée et al. 2011b), either allopatry or sympatry, more rarely parapatry (but see Gavrilets 2004; Gavrilets et al. 2007; Gavrilets and Vose 2007; Thibert-Plante and Hendry 2009, 2011). Several authors have pointed out the necessity to take into account the temporal dimension of speciation because of likely shifts in the geographical arrangement during the process (e.g., Schluter 2001; Rundle and Nosil 2005; Bolnick and Fitzpatrick 2007; Xie et al. 2007; Fitzpatrick et al. 2008; Johannesson 2010). Our model constitutes a step in this direction. In our model, most speciation events, from their initiation to their completion, result from the combination of mechanisms occurring in allopatry (e.g., local adaptation) and in sympatry (e.g., reinforcement). Butlin et al. (2008) and Fitzpatrick et al. (2008, 2009) argued that classifying speciation events into distinct classes (allopatric, parapatric, or sympatric) is unrealistic and potentially misleading. As highlighted by our results, understanding the geographic background at each step of a speciation event is informative because this affects the possible mechanisms influencing change (Rundle and Nosil 2005; Bolnick and Fitzpatrick 2007). In addition, eco-evolutionary mechanisms acting in allopatry and sympatry are not independent: the outcome of one mechanism may define the conditions in which another one proceeds, which may affect its outcome.

CONFRONTATION TO PREVIOUS LITERATURE

Some authors showed that many species can be generated in sympatry alone (e.g., van Doorn et al. 1998; Bolnick and Doebeli 2003; Ito and Dieckmann 2007), but some other authors argued that free recombination and polygenic inheritance with small effect of each allele on the trait value may impede sympatric speciation (e.g., Gavrilets 2003; Coyne and Orr 2004; Waxman and Gavrilets 2005). We incorporated these genetic constraints in our model, thereby impeding sympatric speciation. We also measured diversity without these constraints: in a static, merged landscape, assuming default parameter values (Table 1) except single-locus genetics for all traits ($L_x = L_y = L_a = 1$), sympatric speciation is easy but produces only 2.92 ± 1.28 species on average. This is much lower than diversity reached in a dynamic landscape even with rare sympatric speciation events (Fig. 4, Table 2): some parts of the ecological space, attainable by character displacement or reinforcement, which occur in dynamic landscapes only, are not attainable by sympatric speciation alone.

In the standard scenario of adaptive radiation, explicitly modeled by Gavrilets and Vose (2005, 2009), diversity is generated by repetitive allopatric speciation events and propagated by secondary contacts due to migration (Gavrilets and Losos 2009; Losos and Ricklefs 2009). In this scenario, a subtle balance of migration may be necessary to allow diversification (Heaney 2000; Parent et al. 2008; Losos and Ricklefs 2009). Assuming a too small migration rate, migrant populations are likely to go extinct by demographic stochasticity, or to fail to initiate character displacement (Gillespie et al. 2008; Aguilée et al. 2011a) or reinforcement (Templeton 1981; Aguilée et al. 2011b). On the contrary, a high migration rate may allow the migrant population to persist, but allopatric divergence may be then strongly limited (Coyne and Orr 2004). The effects of "too strong" and "too weak" migration rate to generate a radiation can be compared to special cases of the landscape dynamics in our model. In a static, fragmented landscape with a high migration rate, mating opportunities between individuals born in different sites are frequent, and no radiation is expected. In a dynamic landscape with few fragments at steady state (case 5 of our results), these opportunities are also frequent, and we observed no radiation. Conversely, mating opportunities between individuals born in different sites are rare with both slow dynamics of a landscape with many fragments at steady state (case 2) and with a small migration rate in a static, fragmented landscape. Unlike in the migration scenario, we showed that a radiation is produced in case 2 after a long enough time. In the migration scenario, the size of resident and migrant populations are very asymmetrical, which disfavors maintenance of both populations. In our scenario, the rare secondary contacts involve populations of size of similar order of magnitude, which facilitates character displacement and reinforcement.

Our model was inspired by the landscape dynamics of the Great African Lakes which possibly contributed to the radiation of cichlid fishes (Sturmbauer 1998; Schwarzer et al. 2012). Similar landscape dynamics in other regions may have contributed to produce radiations. Cook (2008) analyzed Madeiran land snail diversity in relation to landscape dynamics. The topology and connectivity of the Madeiran islands changed due to repeated volcanic events, sea level changes, and strong erosion. Cook (2008) suggested that the high snail diversity may result from many opportunities for allopatric divergence and interactions between species at secondary contact. She suggested that biodiversity can be explained using a "rate of geodetic change" to account for landscape changes. She asserted that slow landscape dynamics would generate only limited diversity, and that fast landscape dynamics are likely to induce diversity collapses. Our model gives similar predictions. The "species pump" occurring in dynamic landscapes was also suggested to contribute to explain the diversity of birds in Amazonian forests (Haffer 1969; Terborgh 1992; Haffer 1997; Hill and Hill 2001; Sedano and Burns 2010), butterfly distributions (Colinvaux 1979), and patterns of mammal endemism in Africa (Grubb 1982).

MODEL ASSUMPTIONS AND NATURAL POPULATIONS

We expect the following assumptions of our model to be essential to lead to an adaptive radiation driven by landscape changes. First, the landscape should consist of at least two sites with two different habitat types to allow for allopatric ecological divergence. Second, the distance between ecological optima should be small enough to allow populations to reach the local optimum between two connections of sites. Third, selection should be locally disruptive to allow for the coexistence of several species in sympatry, and for reinforcement and character displacement to occur. Disruptive selection is thought to be a major requirement for adaptive radiation (Rosenzweig 1978; Christiansen 1991; Abrams et al. 1993; Geritz et al. 1997, 1998; Cohen et al. 1999; Ito and Dieckmann 2007; Losos and Ricklefs 2009; Rundell and Price 2009). Fourth, resource distributions should be sufficiently wide for the ecological space to support more than one species per habitat type. Fifth, resource distributions should overlap between habitat types to allow the propagation of local diversity to other sites. This assumption seems consistent with the fact that radiations often occur in narrowly confined regions (Galis and Metz 1998; Schluter 2000; Seehausen 2004). Sixth, a mechanism allowing assortative mating to evolve should exist. We made several other assumptions, either to improve realism of our model (e.g., a multidimensional ecological trait), or to simplify the model interpretation (e.g., one single ecological optimum in merged regions), or to clearly illustrate the allo-sympatric radiation process (e.g., rare sympatric speciation). These other assumptions may either favor (e.g., assortative mating based on ecological traits under disruptive selection) or disfavor (e.g., rare sympatric speciation) diversification, but none of them is expected to be critical to our results. We discuss the most important ones below.

We assumed that when a border isolating two sites disappears, the two sites instantaneously merge into a panmictic unit. More realistically, some individuals might keep feeding in the same site, but sometimes also disperse and mate in the other site. However, the two sites may eventually become merged, because individuals motile enough to mate elsewhere are likely also motile enough to feed elsewhere. We modeled such progressive secondary contact in Aguilée et al. (2011b) with a "window of partial secondary contact" defined as a period of time during which the dispersal rate is reduced compared to panmixia. We found that speciation is facilitated, because intermediate hybrids are produced slower, preventing them to invade the ecologically differentiated populations, which makes reinforcement more efficient. Consequently, we expect a radiation to be generated more easily with progressive secondary contacts than instantaneous ones.

Here, we did not consider incomplete fusions of sites which keep a reduced dispersal rate permanently. As stated previously, the efficiency of evolutionary processes occurring at secondary contact would then depend on the migration rate in a complex manner. Further research is necessary to investigate this situation.

We assumed small population sizes (about 500 individuals for each species), so that demographic stochasticity is significant. With small population size, the populations drift around the local ecological optimum. This may generate new species, or facilitate reinforcement or character displacement at secondary contact. By contrast, the smaller the populations size, the slower their phenotypic evolution. Small population size thus slows down allopatric divergence. We ran simulations with two times higher populations size than the default value and found similar diversification patterns (not shown). The two aforementioned opposite effects thus appear to compensate on average, at least for the range of population sizes explored.

We assumed that each trait is determined by 16 independently segregating loci with small effect of each allele on the trait value, which impedes sympatric speciation (Gavrilets 2003; Coyne and Orr 2004; Waxman and Gavrilets 2005). In addition, small population size strongly delays sympatric speciation (Claessen et al. 2007, 2008; Johansson et al. 2010). Sympatric speciation is thus rare in our model, except following periods of intense hybridization (as when hybrid swarms are generated). We made sympatric speciation unlikely to emphasize the effect of landscape dynamics on diversification, but this assumption might be relaxed: for example, in cichlid fishes of Lake Victoria, traits on which mating is based are determined by one to four loci (Haesler and Seehausen 2005; Magalhaes and Seehausen 2010). This may significantly facilitate sympatric speciation. In dynamic landscapes, with single-locus genetics for all traits ($L_x = L_y = L_a = 1$; default value for the other parameters, Table 1), diversity is generated very quickly and the typical diversity eventually reached is similar (Fig. S1 vs. Fig. 4, panels A and D).

We assumed that assortative mating is based on ecological traits under disruptive selection. Such ecological traits are called magic traits (Gavrilets 2004) and facilitate the evolution of assortative mating (e.g., Dieckmann and Doebeli 1999; Servedio 2000). Magic traits have long been debated in the literature and seem now accepted as possible (Servedio et al. 2011). In the case of cichlid fishes, several ecological traits may act as magic traits (Seehausen and Magalhaes 2010). Seehausen et al. (2008), for example, showed that fish populations living in different light regimes differ in their visual system adaptation. Assortative mating in these populations may be partly due to color assortative mating. Note that sexual selection on body color also contributed to the evolution of assortative mating in this system (Seehausen et al. 1997; Galis and Metz 1998). For the sake of generality, we assumed that choosiness does not depend on the trait of the potential mate. In a model specifically designed for cichlid fishes, Kawata et al. (2007) assumed three independently evolving traits setting choosiness specific to each of three different colors. They found that this correlation does not prevent speciation, which tends to show that our assumption is not critical to our results. We also assumed a very small cost of choosiness, which facilitates speciation (Schneider and Bürger 2006; Kopp and Hermisson 2008). We still expect to observe a radiation if we introduce some moderate cost of choosiness, because (1) as soon as several species appear in a site, competition between them generates strong disruptive selection continuously selecting for assortative mating, and (2) under fast enough landscape dynamics, assortative mating may be maintained by frequent reinforcement events at secondary contact.

Finally, note that our results depend on how the mutation rate scales with the rate of landscape changes (Claessen et al. 2007; Aguilée et al. 2011b): the speed of trait evolution is expected to be proportional to the product of the mutation rate with the phenotypic variance. The high mutation rate we used (10^{-3}) may speed up diversification relative to the rate of landscape changes. However, we have offset it with a small expected phenotypic variance ($s_x^2 = s_y^2 = 0.0016$, $s_a^2 = 0.01$). Using a lower mutation rate (10^{-5}), a higher expected phenotypic variance ($s_x^2 = s_y^2 = 0.01$, $s_a^2 = 0.04$), and a lower number of loci (6), we observed similar patterns of diversification, although the radiation proceeds slower (Fig. S2 vs. Fig. 4, panels A and D).

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Supporting Information

Additional Supporting information may be found in the online version of this article at the publisher's website:

Appendix S1: Methods for simulations.
Appendix S2: Methods for diversity estimation.
Appendix S3: Methods to compute the measures used in the Results section.
Appendix S4: Supplementary Figures.
Figure S1: Time series of γ diversity with single-locus genetics for all traits.
Figure S2: Time series of γ diversity with lower mutation rate.

Appendices for
"Adaptive radiation driven by the interplay of eco-evolutionary and landscape dynamics"

Robin Aguilée, David Claessen and Amaury Lambert

S1   Methods for simulations

Our stochastic model is simulated using Gillespie (1977)'s algorithm in continuous time. It a mathematical property of Gillespie's algorithm that the landscape dynamics and the population dynamics are independent. At any time, four events can happen: the birth of an individual (occurring at rate $rN(t)$ where $N(t)$ is the total population size), the death of an individual (rate $\sum_{i=1}^{N(t)} d(z_i)$ where $d(z_i)$ is defined by Eq. (1)), the disappearance of a border (rate $cN_{\mathrm{a}}(t)$ where $N_{\mathrm{a}}(t)$ is the number of existing borders), and the appearance of a border (rate $fN_{\mathrm{d}}(t)$ where $N_{\mathrm{d}}(t)$ is the number of disappeared borders). We pick the time until the next event from an exponential distribution with mean $1/(rN(t) + \sum_{i=1}^{N(t)} d(z_i) + cN_{\mathrm{a}}(t) + fN_{\mathrm{d}}(t))$. The occurring event is then randomly chosen proportionally to the rate of each possible event.

Initially, each border is independently present with probability $f/(f + c)$, which corresponds to the stationary state of the landscape. The central site is defined as a habitat P, the habitat type of each satellite site is randomly chosen at the beginning of each simulation run as a habitat either R or S. Each site is initialized with K^* individuals whose sex is randomly chosen (assuming a balanced sex-ratio) and whose alleles values at each locus determining trait k ($k \in (x, y, a)$) are chosen in a centered normal distribution with standard deviation s_k.

We measure time in generations: the generation time is equal to one time unit of the simulation real time divided by the *per-capita* death rate. As the death rate differs between individuals, we approximate it by the *per-capita* birth rate, which is expected to have the same value when the population is at its ecological equilibrium.

The simulation program is coded with the C language using the GNU Scientific Library (Galassi et al., 2009) for random number generation. The computation of diversity is coded with the R language (R Development Core Team, 2010). Source code is available on Dryad repository.

S2 Methods for diversity estimation

Our estimation of diversity is expressed as a number of species, in the sense of the biological species concept (Mayr, 1942). We proceed with the three following steps.

Step (i): definition of clusters of individuals whose ecological traits are close. The phenotypic space (x, y) is divided into cells of area $s_x \times s_y$. We define "well-occupied cells" as cells whose density is higher than the mean density computed over non-empty cells. Neighboring well-occupied cells form a phenotypic cluster (diagonal cells are considered as neighboring). Individuals from other cells belong to the cluster whose phenotypic center is the closest.

Step (ii): evaluation of the level of reproductive isolation between each pair of clusters. For each pair of clusters, we use Eq. (3) to compute the mean mating probability $\bar{\pi}$ of individuals randomly sampled from distinct clusters.

Step (iii): computation of the number of distinct species. Two distinct phenotypic clusters are considered as reproductively isolated when $\bar{\pi}$ is below the threshold $v = 0.01$. A continuous chain of clusters formed by pairs of reproductively non-isolated clusters defines a species (cohesion relaxed interpretation of the biological species concept, Gonzàlez-Forero, 2009).

Local (α) diversity is computed by applying this method independently in each of the $n_s + 1$ sites, then averaging the $n_s + 1$ values. To evaluate total (γ) diversity, we apply the above method taking into account all individuals of the metapopulation together. This virtually corresponds to a secondary contact of all individuals. If such instantaneous secondary contact really occurred, new competitive interactions and/or habitat changes would possibly lead evolutionary processes to change the number of species. Therefore, our estimation of γ diversity does not indicate the number of species at the evolutionary equilibrium; it indicates the instantaneous number of species. Note that our method implies that two phenotypic clusters in a same site can be considered as two distinct species when computing α diversity, but as the same species when computing γ diversity, if an intermediate phenotypic cluster exists in another site.

Step (i) of the above method ensures to exclude rare individuals isolated from others individuals in the ecological space from being considered as a full-fledged population. This avoids two issues: considering as a species a single individual unusually far from other individuals in the ecological space, and considering as the same species two phenotypic clusters with a stable and high level of reproductive isolation between them because of a single, exceptional hybrid.

Step (iii) uses a threshold v whose value is arbitrarily fixed. Gavrilets (1999) used an analogous threshold to distinguish species. He showed that the number of species is weakly dependent on its value, even when the threshold value varies by several orders of magnitude. We checked that this statement is valid for our simulations: using $v = 0.001$ instead of our default value ($v = 0.01$) in some generic simulations, there were no detectable qualitative change in the results, and very weak quantitative effects (results not shown).

S3   Methods to compute the measures used in the Results section

Typical γ diversity. For each simulation replicate, we compute the γ diversity averaged over time, ignoring the 50,000 first generations in order to exclude the initial diversification. The typical γ diversity is then estimated as the average over simulation replicates of these γ diversities.

Time to reach typical γ diversity. For each simulation replicate, we compute the number of generations until γ diversity reaches its typical level. The time to reach typical γ diversity is then estimated as the average over simulation replicates of these numbers of generations.

Variance of the typical γ diversity over time. For each simulation replicate, we compute the variance of the γ diversity over time, from the time γ diversity reaches its typical level to the end of the simulation. The variance of the typical γ diversity over time is then estimated as the average over simulation replicates of these variances.

Allopatric divergence. For each simulation replicate, at each time, we compute the ecological distance between pairs of populations from geographically isolated regions as the distance between the centers of their ecological trait distributions. This ecological distance is computed only between pairs of populations from geographically isolated regions with different ecological optima, because no allopatric divergence is expected between geographically isolated regions with the same ecological optimum. For each simulation replicate, at each time, all ecological distances computed are averaged. Allopatric divergence is then estimated as the average over time and over simulation replicates of these mean ecological distances.

Minimal ecological distance. For each simulation replicate, at each time after typical γ diversity is reached, we compute the ecological distance between all pairs of species from all sites of the landscape combined as the distance between the center of their ecological trait distribution. At each time step, we take the minimum of all the computed distances. The minimal ecological distance between species is then estimated as the average over time and over simulation replicates of these ecological distances. This measure is to compare to the minimal ecological distance between sympatric species, which is computed similarly but considering ecological distances between sympatric species only.
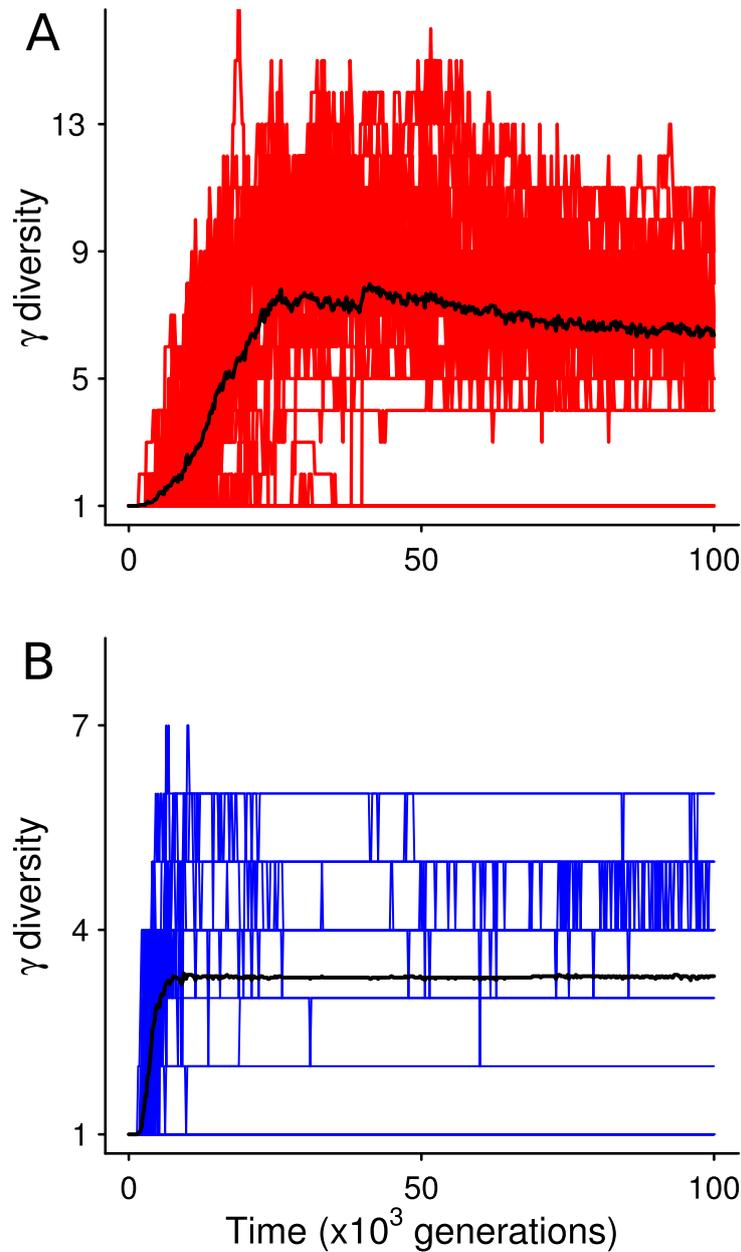
S4   Supplementary Figures

Figure S1: Time series of γ diversity. Panel A: landscape dynamics of type 1, as defined in section "Types of landscape dynamics". Panel B: landscape dynamics of type 3. Colored time series are the 50 simulation replicates superimposed. The black time series are their average over time. Parameter values: default parameter values (Table 1) except single-locus genetics for all traits ($L_x = L_y = L_a = 1$). The total population size varies from about 5000 to 7000 individuals, depending of the number of species. With single-locus genetics, the initiation of sympatric speciation (i.e. the emergence of phenotypic clusters) is very quick. Because many phenotypic clusters appear simultaneously (typically, from 6 to 12 in these simulations), the evolution of reproductive isolation between them can be very long, longer than 10^5 generations. This explains why some simulation replicates show no diversification.
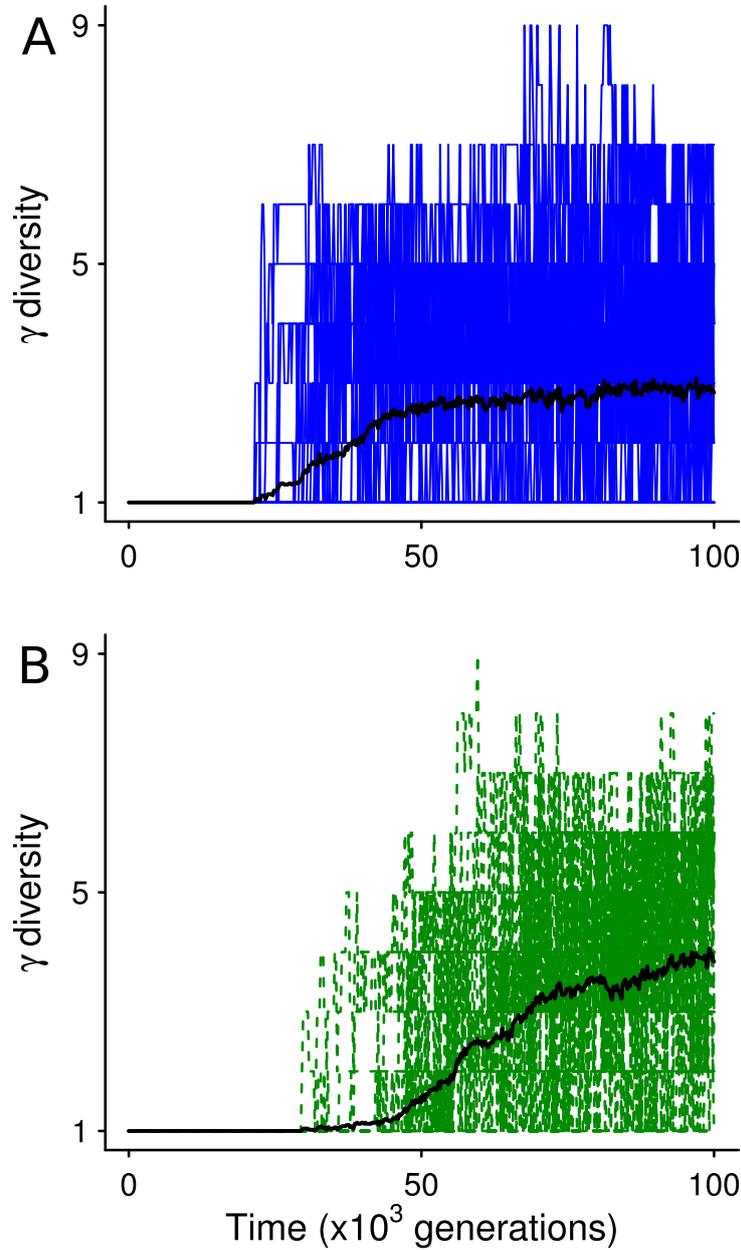
Figure S2: Time series of γ diversity. Panel A: landscape dynamics of type 3, as defined in section "Types of landscape dynamics". Panel B: landscape dynamics of type 4. Colored time series are the 50 simulation replicates superimposed. The black time series are their average over time. Parameter values: default parameter values (Table 1) except lower mutation rate ($\mu_x = \mu_y = \mu_a = 10^{-5}$), higher expected phenotypic variance ($s_x^2 = s_y^2 = 0.01$, $s_a^2 = 0.04$), and lower number of loci ($L_x = L_y = L_a = 6$). The total population size varies from about 4000 to 6000 individuals, depending of the number of species.

5

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