

How Ecology and Landscape Dynamics Shape Phylogenetic Trees

FANNY GASCUEL^{1,2,3,*}, RÉGIS FERRIÈRE^{3,4}, ROBIN AGUILÉE⁵, AND AMAURY LAMBERT^{1,6}

¹Center for Interdisciplinary Research in Biology, CNRS UMR 7241, Collège de France, Paris, France; ²Sorbonne Universités, UPMC Univ Paris 06, CNRS UMR 7625, Laboratoire Écologie et Évolution, Paris, France; ³Institut de Biologie de l'Ecole Normale Supérieure, CNRS UMR 8197, École Normale Supérieure, Paris, France; ⁴Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ USA; ⁵Laboratoire Évolution et Diversité Biologique, CNRS UMR 5174, Université Paul Sabatier, Toulouse, France; and ⁶Sorbonne Universités, UPMC Univ Paris 06, CNRS UMR 7599, Laboratoire Probabilités et Modèles Aléatoires, Paris, France

*Correspondence to be sent to: Center for Interdisciplinary Research in Biology, Equipe Stochastic Models for the Inference of Life Evolution, Collège de France, 11 place Marcelin Berthelot, 75005 Paris, France; E-mail: fanny.gascuel@college-de-france.fr.

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Abstract.—Whether biotic or abiotic factors are the dominant drivers of clade diversification is a long-standing question in evolutionary biology. The ubiquitous patterns of phylogenetic imbalance and branching slowdown have been taken as supporting the role of ecological niche filling and spatial heterogeneity in ecological features, and thus of biotic processes, in diversification. However, a proper theoretical assessment of the relative roles of biotic and abiotic factors in macroevolution requires models that integrate both types of factors, and such models have been lacking. In this study, we use an individual-based model to investigate the temporal patterns of diversification driven by ecological speciation in a stochastically fluctuating geographic landscape. The model generates phylogenies whose shape evolves as the clade ages. Stabilization of tree shape often occurs after ecological saturation, revealing species turnover caused by competition and demographic stochasticity. In the initial phase of diversification (allopatric radiation into an empty landscape), trees tend to be unbalanced and branching slows down. As diversification proceeds further due to landscape dynamics, balance and branching tempo may increase and become positive. Three main conclusions follow. First, the phylogenies of ecologically saturated clades do not always exhibit branching slowdown. Branching slowdown requires that competition be wide or heterogeneous across the landscape, or that the characteristics of landscape dynamics vary geographically. Conversely, branching acceleration is predicted under narrow competition or frequent local catastrophes. Second, ecological heterogeneity does not necessarily cause phylogenies to be unbalanced—short time in geographical isolation or frequent local catastrophes may lead to balanced trees despite spatial heterogeneity. Conversely, unbalanced trees can emerge without spatial heterogeneity, notably if competition is wide. Third, short isolation time causes a radically different and quite robust pattern of phylogenies that are balanced and yet exhibit branching slowdown. In conclusion, biotic factors have a strong and diverse influence on the shape of phylogenies of ecologically saturating clades and create the evolutionary template in which branching slowdown and tree imbalance may occur. However, the contingency of landscape dynamics and resource distribution can cause wide variation in branching tempo and tree balance. Finally, considerable variation in tree shape among simulation replicates calls for caution when interpreting variation in the shape of real phylogenies. [adaptive radiation; allopatric speciation; competition; eco-evolutionary feedbacks; ecological speciation; geographic isolation; Macroevolution; phylogeny]

How species diversity originates and how it changes across multiple scales of time and space is a perennial question in evolutionary biology. To infer the history of species diversification, reconstructed phylogenies can be fitted by mathematical models of tree growth, such as the pure-birth process (also called Yule process; Yule 1925), which assumes that the species tree is only generated by constant-rate speciation; and the birth–death process (Kendall 1948; Raup et al. 1973), which assumes that the species tree is generated by speciation and extinction events occurring at constant rates per lineage. Because the Yule and birth–death processes assume constant evolutionary rates, they are referred to as null models of phylogenetic tree growth.

To evaluate the hypothesis that a given clade diversified at constant speciation and extinction rates, the shape of the clade's reconstructed phylogeny (i.e., tree of extant species) can be compared to that of trees generated under null models (Mooers and Heard 1997). There are two main properties that characterize phylogenetic tree shape: branching tempo and (im)balance. Branching tempo refers to the distribution of relative branching times from the root

to the tips of the tree; it thus reflects variation in the rate of lineage accumulation through time. Imbalance refers to the distribution of branchings among subclades: diversification rates that differ between subclades can lead to unbalanced trees, while homogeneous rates lead to balanced trees.

Empirical phylogenies have been shown to often differ from trees generated by the null models both in terms of branching tempo and balance. Real phylogenies tend to be unbalanced (e.g., Guyer and Slowinski 1991; Heard 1992; Guyer and Slowinski 1993; Slowinski and Guyer 1993; Mooers 1995; Purvis 1996; Mooers and Heard 1997; Blum and François 2006), and branching tends to slow down (e.g., Nee et al. 1992; Zink and Slowinski 1995; Lovette and Bermingham 1999; Pybus and Harvey 2000; Rüber and Zardoya 2005; Kozak et al. 2006; Seehausen 2006; Weir 2006; McPeek 2008; Phillimore and Price 2008; Rabosky and Lovette 2008a; Jönsson et al. 2012).

Statistical models of phylogenetic trees have been developed to characterize variations in evolutionary rates of speciation and extinction, through time and/or among subclades (Sanderson and Donoghue 1996; Ricklefs 2007; Stadler 2011; Pyron and Burbrink

2013). These models, which consider either diversity-dependent (Rabosky and Lovette 2008b; Etienne et al. 2012), trait-dependent (Maddison et al. 2007; FitzJohn 2010), or time-dependent evolutionary rates (Alfaro et al. 2009; Morlon et al. 2011; Stadler 2011), fit empirical patterns of diversification better than the null, constant-rates models. However, the question of the mechanisms causing changes in evolutionary rates through time (possibly mediated by change in diversity) or among clades (possibly mediated by character differentiation), remains out of reach of such models that are phenomenological in essence (Nee 2006; Pyron and Burbrink 2013). A major challenge is now to identify what mechanisms are responsible for variations in evolutionary rates through time and across clades.

More mechanistic models of evolutionary diversification, either species- or individual-based, have recently been developed (e.g., Doeblei and Dieckmann 2003; Gavrilets and Vose 2005; McPeek 2008; Aguilée et al. 2011; Pontarp et al. 2012; Aguilée et al. 2013) with the goal of investigating how specific components of the diversification process influence phylogenetic tree shape. Geographical structure involved in allopatric speciation (Pigot et al. 2010), demographic asymmetry at speciation (comparing point mutation, where new species arise as singleton lineages, and random fission, where ancestral species are randomly cleaved into two daughter species; Davies et al. 2011), and ecological differentiation at speciation (McPeek 2008), have been shown to influence the shape of reconstructed species trees; conditions were found for these processes that can lead to branching slowdown and/or unbalanced topology. However, these models describe the process of speciation only phenomenologically, as opposed to speciation being an emergent phenomenon driven by underlying genetic and ecological mechanisms at the individual level. Thus, in these models the dynamics of speciation (rate, location) were assumed, rather than being an output of the model.

A critical role for individual-level ecological processes in species diversification has long been envisioned and discussed ever since Darwin (Darwin 1859; Simpson 1953; Stanley 1979; Grant 1986; Schlüter 2000): interactions between organisms and their environment may drive directional selection (e.g., Grant 2003), and interactions among organisms may generate disruptive selection (through inter- or intraspecific competition, or through predation; e.g., Dieckmann and Doeblei 1999; Bailey et al. 2013). According to the Red Queen view of evolution (Van Valen 1973), ecological processes may even drive diversification. Thus, there is a need to develop macroevolutionary models that explicitly take into account ecological processes, and this has been identified as a major challenge at the interface of evolutionary and ecological theory (Pigot et al. 2010; McInnes et al. 2011; Fritz et al. 2013; Pyron and Burbrink 2013; Wang et al. 2013; Morlon 2014).

The conventional view is indeed that ecological niche filling is responsible for branching slowdown

(e.g., MacArthur 1972; Rosenzweig 1978; Pimm 1979; Walker and Valentine 1984; Nee et al. 1992; Lovette and Bermingham 1999; Weir 2006; Phillimore and Price 2008; Jønsson et al. 2012). Alternative non-ecological hypotheses (reviewed in Moen and Morlon 2014) include an increase in genetic constraints over time (Gavrilets and Losos 2009) and a nonrandom acceleration of extinction (Zink and Slowinski 1995, although the latter may have an ecological mechanistic underpinning). Ecological niche filling is supposed to slow down diversification through an increase in the number of species competing for limited resources (Mayr 1942, 1947; Simpson 1953; Schlüter 2000); by contrast, in the early stage of diversification the limited number of competitors is expected to strengthen directional and disruptive selection (Schlüter 2000, 2001). Furthermore, spatial heterogeneity in the availability and width of ecological niches is expected to impact species diversity in subclades evolving locally in space, and thus to explain the imbalance of the species trees (e.g., Simpson 1944; Rosenzweig 1995; De Queiroz 2002; Purvis et al. 2011). Alternative hypotheses for tree imbalance include the effect of key innovations (e.g., Simpson 1953; Heard and Hauser 1995; Phillimore et al. 2006; Jønsson et al. 2012; Magnuson-Ford and Otto 2012), sexual selection (Darwin 1871; Barraclough et al. 1995; Mitra et al. 1996), and demographic asymmetries between mother and daughter lineages at speciation (Davies et al. 2011).

Does the ubiquitous pattern of phylogenetic branching slowdown and imbalance call for ecological niche filling and spatial heterogeneity in ecological features as the main explanation, and does this lend weight to the biotic (Red Queen) view of species diversification? Here we aim at testing *in silico*: (i) whether ecological niche filling is the general explanation for the tendency of branchings to decelerate in phylogenetic trees; (ii) whether wide competition limiting the number of available ecological niches accentuates this slowdown; and (iii) whether spatial heterogeneity in ecological features is the general explanation for the tendency of clade diversification to proceed at different rates in different subclades, thus generating unbalanced phylogenetic trees.

We use an individual-based model of adaptive radiation driven by ecological speciation. Individuals are characterized by their ecological phenotype, which drives exploitative competition; heritable variation in the ecological phenotype fuels the processes of within-species local adaptation (anagenesis) and speciation (cladogenesis) in a dynamic landscape where local communities can split and fuse repeatedly through evolutionary time, thus allowing not only allopatric speciation, secondary contact, character displacement, reinforcement, but also hybridization. This dynamic landscape allows us to investigate how the effects of biotic factors on macroevolutionary patterns are altered by changes in the abiotic environment that occur on longer timescales (e.g., climatic changes or tectonic activity). The latter are indeed also recognized to influence diversification (Keast 1961; Cracraft 1986;

Barnosky 1999; Ezard et al. 2011), by striking lineages at random and potentially causing speciation or extinction (“Court Jester” hypothesis, Barnosky 1999).

We consider three aspects of environmental changes formulated in terms of landscape dynamics. First, we explore the role of the pace of landscape dynamics, involving the recurrent fusion and fragmentation of geographical sites over time. Landscape dynamics are known to play a major role in diversification (Mayr 1942; Greenwood 1965; Rossiter 1995; Aguilée et al. 2013), due to the recurrence of ecological divergence in allopatry followed by reinforcement or character displacement at secondary contact. Second, we investigate the effect of the time in isolation, measured as the expected proportion of time that two adjacent sites spend in isolation of one another. Third, we address the influence of the frequency of local catastrophes that strike geographical sites at random and cause the extinction of all populations living in that site. Local catastrophes tend to keep metapopulation size below carrying capacity, hence potentially limiting the ecological and evolutionary effects of competition.

These analyses provide new insights into the causal relationship between ecological niche filling and spatial environmental heterogeneity on the one hand, and the branching tempo and balance of phylogenetic trees on the other. By comparing our theoretical results to existing empirical data, we discuss how biotic and abiotic factors may interact and together shape the branching pattern of real phylogenetic trees.

MATERIALS AND METHODS

Model Overview

We use Aguilée et al.’s (2013) model of diversification. Hereafter, we highlight key features of the model; for a fuller description, see Aguilée et al. (2013). The model describes the dynamics of a community of competitively interacting species that inhabit a patchy landscape. Organisms are diploid and reproduce sexually. The model tracks the population dynamics of each species and their spatial distribution in a patchy landscape that varies in time and space. The model integrates biotic processes that operate at the level of individuals: individual birth and death, local interactions between individuals, dispersal; and abiotic processes that operate at the level of patches: fragmentation or fusion of extant patches that drive the landscape dynamics; heterogeneity in resource distribution that translates into among-patch variation in carrying capacity.

The community history of species origination and species loss emerges from the joint operation of the individual-level biotic and patch-level abiotic processes. Local adaptation drives anagenesis, and cladogenesis is driven by the evolution of reproductive isolation. The community can lose species because of extinctions, which can be due to demographic stochasticity, competitive exclusion, hybridization, or environmental catastrophes. Thus, speciation and extinction rates are

not predefined; they are model outputs. From one ancestral species the model predicts the growth of the whole species tree, and how the tree is shaped by the underlying processes and their parameters.

Individual-level Processes

We assume that resources vary along gradients on two spatial dimensions, and that the resource utilization strategy of an individual is described by two ecological traits, x_1 and x_2 , one for each spatial dimension. The pair (x_1, x_2) is the individual’s “ecological phenotype”. Individuals also express a ‘choosiness trait’ a , which measures the degree to which ecological phenotypic similarity influences the probability of mating; choosiness can favor mating between either more similar or more dissimilar ecological phenotypes. All three traits are genetically variable. They are determined by L_k diploid, additive quantitative loci on autosomal chromosomes, where k denotes x_1 , x_2 , or a . We use $L_k = 16$, which is large enough to make sympatric speciation unlikely (Gavrilets 2003; Coyne and Orr 2004; Waxman and Gavrilets 2005).

Local (i.e., within each patch) population growth is assumed to be logistic, with competition for resources being both locally density-dependent (Roughgarden 1972) and frequency-dependent, that is, stronger between individuals with more similar ecological traits (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2003). The birth rate of each individual is assumed to be constant. The death rate depends on the local carrying capacity and on the strength of local competition. In each geographical site, the carrying capacity function, which models a continuous distribution of resources, is a Gaussian function with maximum K at phenotype (x_1^*, x_2^*) , called the ecological optimum of the site, and standard deviation σ_K . The strength of local competition is the sum of the competition strengths with all other individuals of the same patch (or set of connected patches - see below); competition strength between each pair of individuals is also given by a Gaussian function of the Euclidian distance between their ecological phenotypes, with maximum value one when the distance is zero, and standard deviation σ_C . The standard deviation of the carrying capacity function, σ_K , is chosen to be larger than that of the competition kernel, σ_C , to ensure that ecological optima would be “evolutionary branching points” in the corresponding trait-substitution sequence model for an asexual population (Geritz et al. 1998; Dieckmann and Doebeli 1999; Vukics et al. 2003; Doebeli and Ispolatov 2010). Gaussian kernels have been widely used to model competition, but also criticized for introducing structural instability in deterministic models of resource use evolution (Barton and Polechová 2005; Gyllenberg and Meszéna 2005; Leimar et al. 2008). By including multiple sources of stochasticity (in individual life history, mutation, dispersal, and landscape dynamics), our results should be immune to the spurious effects of strictly Gaussian competition kernels.

Reproduction is sexual. We use the same mating probability function as in Aguilée et al. (2013): a Gaussian function with the minimum biological realism required, where mating probability depends on the similarity in the ecological phenotypes of the two partners and on the choosiness of the more choosy one (either toward similarity or dissimilarity). If mating is rejected, another potential mate is drawn at random and the process is repeated until mating succeeds, or until 50 potential mates have been tried. The cost of choosiness is thus assumed to be small (Schneider and Bürger 2006; Kopp and Hermisson 2008), facilitating the evolution of assortative mating. When mating occurs, the offspring sex is determined randomly assuming a balanced sex ratio; the offspring ecological and choosiness traits are determined from the random independent segregation of the L_k parental loci that code for each trait k ($k=x_1, x_2$, or a). Mutation occurs at each locus with probability μ_k and the mutant allelic value is drawn from a normal distribution with mean equal to the parental allelic value and with standard deviation $\sigma_{\mu_k} \sqrt{2L_k}$.

Landscape Dynamics

The metacommunity evolves in a structured landscape, made of $n \times n$ sites distributed over a two-dimensional grid. Each site is characterized by a different ecological optimum (x_1^*, x_2^*), with x_1^* and x_2^* increasing by a constant amount δ_x between adjacent sites in either direction. The landscape is dynamic in the sense that sites undergo fragmentation and fusion, causing the repeated alternation of allopatry and sympatry. Fragmentation is due to barriers that appear between adjacent sites at rate f ; fusion is due to extant barriers disappearing at rate c . When a set of sites is connected, migration occurs at birth as in the island model (Hanski and Gaggiotti 2004), with equal probability for the offspring to reach any of the connected sites. We, however, also investigated results under another version of the model, where migration is more likely toward the sites where the offspring's parents are located than toward other sites, but this led to similar phylogenetic tree shapes (see online Appendix 1 available as Supplementary Material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>). Finally, our model incorporates local catastrophes that strike sites at random and cause the extinctions of all populations present in the site. The rate of local catastrophe is denoted by cr .

Delineating Species and Following Their Evolutionary History

We delineate species using De Queiroz's (2007) unified concept, considering species as "separately evolving metapopulation lineages"—metapopulations (sets of connected populations) that evolve through time independently from other populations. We first identify populations by grouping all individuals

with close ecological traits (x_1, x_2), as in Aguilée et al. (2013). Then, we cluster these populations into sets of independently evolving metapopulations by calculating the probability of reproductive isolation between each pair of populations (Mayr 1963): each set of populations that can interbreed (probabilities of reproductive isolation below a threshold $thr_{ri}=99\%$) but are reproductively isolated from other populations (probabilities of reproductive isolation above thr_{ri}), is considered to be a species. We compute probabilities of reproductive isolation using the same function as that used for mating between individuals, but using the average values of traits in each population, \bar{x}_1, \bar{x}_2 , and \bar{a} . This approximation reduces computation time significantly while having no major effect on our results (online Appendix 2 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>).

To follow the evolutionary history of species, at each time step t (every 100 generations, with similar results as 10 generations - see online Appendix 3 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>) we determine the N_t existing species $[S_t^{(i)}]_{i \in \{1, \dots, N_t\}}$ as explained above, and then determine how they descend from the species existing at the previous time step, $[S_{t-1}^{(j)}]_{j \in \{1, \dots, N_{t-1}\}}$. Descent relationships are established by comparing the phenotypic traits of species and populations at time t to those at time $t-1$, and by minimizing Euclidian distances between these average traits. Our method ensures that: (i) each species keeps the same identity as long as it remains reproductively isolated from other species, even if its phenotype evolves; (ii) speciation can happen through differentiation of a species into various reproductively isolated populations; (iii) extinction can happen when a population reaches a very small size or through species hybridization; and (iv) descent relationships during hybridization are consistent with probabilities for each species to transmit its genotypes to the future lineage. Further details on how we delineate species and follow their evolutionary history can be found in the online Appendix 4 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>.

Simulating Phylogenies and Analysing Their Shape

Diversification was initiated from one ancestral species, spread over all geographical sites (150 individuals per site). The ecological and choosiness traits (x_1, x_2 , and a) of this species were determined by L_k , $k \in \{x_1, x_2, a\}$, diploid loci randomly chosen in a Gaussian distribution centered at zero. The ancestral species was, therefore, adapted to the geographical site with intermediate ecological optimum (x_1^*, x_2^*) in the two dimensions of the environmental gradient. This prevents any border effects in the initiation of diversification, and represents a wide range of empirical situations leading to eco-evolutionary diversification.

TABLE 1. Parameter values and symbols used in this study, except if a different value is given in the legends

Parameter	Definition	Default value
r	Per-capita birth rate	1
L_k	Number of loci coding each trait k	16 (loci)
μ_k	Mutation probability at each locus	0.001
$\sigma_{\mu_x}^2$	Expected phenotypic variance of trait x	0.0016
$\sigma_{\mu_a}^2$	Expected phenotypic variance of trait a	0.01
K	Carrying capacity at the ecological optimum in each site	150 (individuals)
σ_K	Standard deviation of the maximum carrying capacity per site	1.0
σ_C	Standard deviation of the competition kernel	0.4
n^2	Number of sites in the landscape	9
δ_x	Difference in optimal trait values between adjacent sites	1.0
f	Rate of border appearance	10^{-3} (birth rate)
c	Rate of border disappearance	$5 \cdot 10^{-5}$ (birth rate)
cr	Rate of catastrophic local community extinction	0 (birth rate)

Indeed, once a key innovation (novel phenotypic trait that brings the ability to invade new ecological niches) arose, all the surrounding landscape may potentially offer space and ecological niches for new species to evolve, and thus many species may originate from the ancestral species that acquired the innovation (Simpson 1944, 1953; MacArthur 1972; Walker and Valentine 1984; Schlüter 2000). This sequence of events may also occur following the colonization of new geographical areas with few ecological competitors. We nonetheless studied the influence of border effects, by considering an ancestral species adapted to marginal ecological conditions: results show that border effects also influence phylogenetic tree shape (see online Appendix 5 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>).

For each set of parameters, we simulated the process of diversification for 100,000 generations, running 50 replicates. Not all simulations resulted in successful adaptive radiations: in up to 60% of them, diversification was initiated but failed at some point in time due to the hybridization of all species. This diversity collapse results from the hybridization of two ecologically close species, which increases their phenotypic variance and decreases their level of assortative mating, triggering a cascade of hybridization events throughout the metacommunity. Hybrid collapses have been observed in previous models (Gilman and Behm 2011; Aguilée et al. 2013), and are suspected to occur in nature (Seehausen 2004; Vonlanthen et al. 2012). Here, they are expected to occur at some (possibly very large) time in every single simulation, because of the absence of any mechanism that would prevent species to hybridize. In nature, species are expected to evolve irreversible genetic incompatibilities, which prevent them from hybridizing. However, accounting for such long-term reproductive isolation mechanism does not have any noticeable effect on our results (see online Appendix 6 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>). This is because in simulations without hybrid collapse,

differentiated species never hybridize (if they do so, rapid hybrid collapse always occurs as a result).

Steady state in number of individuals and number of species was typically reached after 30,000 to 50,000 generations. This is much more rapid than typically observed in adaptive radiations (Schlüter 2000), and reflects high mutation rates (see Table 1; similar as in previous individual-based models of diversification, Dieckmann and Doebeli 1999; Gavrilets and Vose 2005; Pontarp et al. 2012; Aguilée et al. 2013). Such high mutation rates make it possible to observe species diversification in reasonable computational time, and are not expected to affect the overall species tree shapes, at least in this model. On the one hand, the speed of phenotypic trait evolution depends on the product of the mutation rate with the phenotypic variance, and thus similar diversification patterns can be observed with smaller mutation rates and higher expected phenotypic variance (e.g., with $\mu_{x_1} = \mu_{x_2} = \mu_a = 10^{-5}$, $\sigma_{\mu_{x_1}}^2 = \sigma_{\mu_{x_2}}^2 = 0.01$, $\sigma_{\mu_a}^2 = 0.04$, and $L_{x_1} = L_{x_2} = L_a = 6$; Aguilée et al. 2013). On the other hand, patterns of species diversification depend on how the rate of phenotypic trait evolution scales with the rate of landscape dynamics (Claessen et al. 2007; Aguilée et al. 2011): similar patterns of diversification can also be observed on longer temporal scales with smaller mutation rates given smaller rates of landscape dynamics. At steady state, most simulated metacommunities contained 12 to 70 different species for a total of 1800 to 9000 individuals.

For each full-run simulation, we extracted the tree of all extant species every 100 generations and characterized its shape both in terms of branching tempo and balance. We analysed the branching tempo of phylogenetic trees by computing the γ statistic, which tests for departures from a time-homogeneous, lineage-based pure-birth process of diversification (Cox and Lewis 1966; Pybus and Harvey 2000). In “tippy” trees, in which nodes are concentrated close to the present (due to an increase in the rate of lineage accumulation toward the present), γ is positive; in “stemmy” trees, in

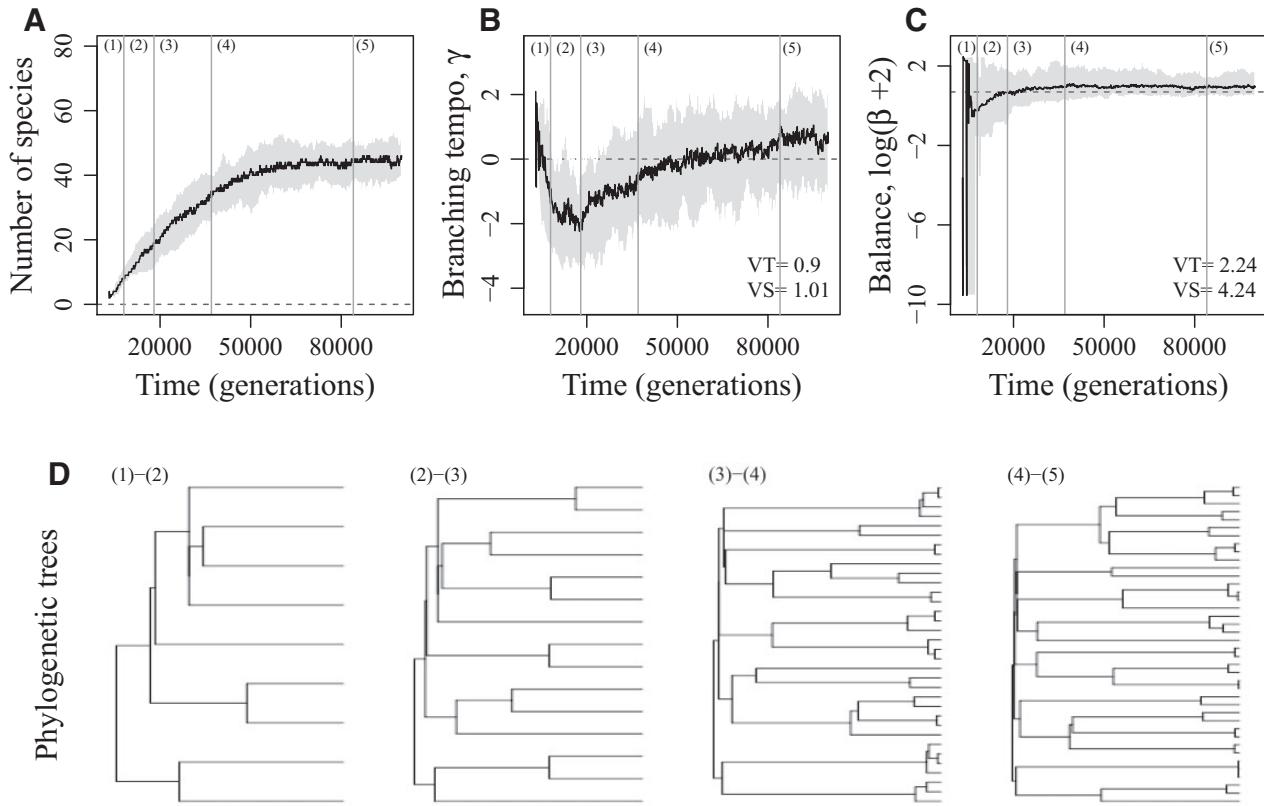


FIGURE 1. Species diversity and phylogenetic tree shape (branching tempo γ and balance β) as a function of time. Time is measured from the common ancestor's introduction in the landscape. Simulations were replicated 50 times. Top row: Black lines give median values; 95% confidence interval shown in gray. Dashed horizontal lines indicate $\gamma=0$ and $\beta=0$. VT and VS give the average variance, respectively over time (corrected according to the median among simulation replicates) and among simulation replicates. Vertical gray lines and associated labels highlight five different stages of γ and β variation across time. Bottom row: Examples of species trees corresponding to four stages of diversification. Competition parameters: $\sigma_C = 0.4$, $\sigma_K = 1.1$. See Table 1 for other parameter values.

which nodes are concentrated close to the base (due to a slowdown in the rate of lineage accumulation toward the present), γ is negative (Pybus and Harvey 2000). The γ statistic has been used extensively in macroevolutionary studies (e.g., Ricklefs 2007; McPeek 2008; Phillimore and Price 2008; Rabosky and Lovette 2008b; Liow et al. 2010; Quental and Marshall 2010; Davies et al. 2011); we were thus able to compare our results to those of previous theoretical studies and empirical estimates. Although γ values, as well as their variability, were shown to decrease with clade size (Pybus and Harvey 2000; McPeek 2008; Boettiger et al. 2012), it should not affect the interpretation of our results, as the latter reveal on the contrary an increase in γ values with age and with species number at steady state (Figs. 1–3).

We analysed the balance of phylogenetic trees by calculating the β statistic, which is the β value that maximizes the likelihood in the β -splitting model of clade growth (Aldous 1996, 2001; Blum and François 2006). This statistic allows one to compare the topology of trees with different numbers of tips (Aldous 1996), and has been widely used to describe tree balance (Blum and François 2006; Pigot et al. 2010; Davies et al. 2011).

Yule trees (pure-birth process) have $\beta=0$, trees more unbalanced than Yule trees have $\beta<0$ and trees less unbalanced than Yule trees have $\beta>0$ (Yule 1925).

Finally, for both statistics γ and β , we computed a measure of variance over time, VT, and a measure of variance among simulation replicates, VS. VT is the mean among simulation replicates of the variance of the difference between the statistic and its median value (calculated on all simulation replicates at the same time step) taken over all time steps. When VT is high, in each simulation the statistic tends to exhibit high temporal variation around its median value among simulation replicates. VS is the mean over time of the variance of the statistic among simulation replicates.

Testing the Effect of Competition and Interaction with Abiotic Factors

Default parameter values are given in Table 1. They were chosen to enable diversification and span a broad range of possible effects on phylogenetic tree shapes, while keeping computational time under control.

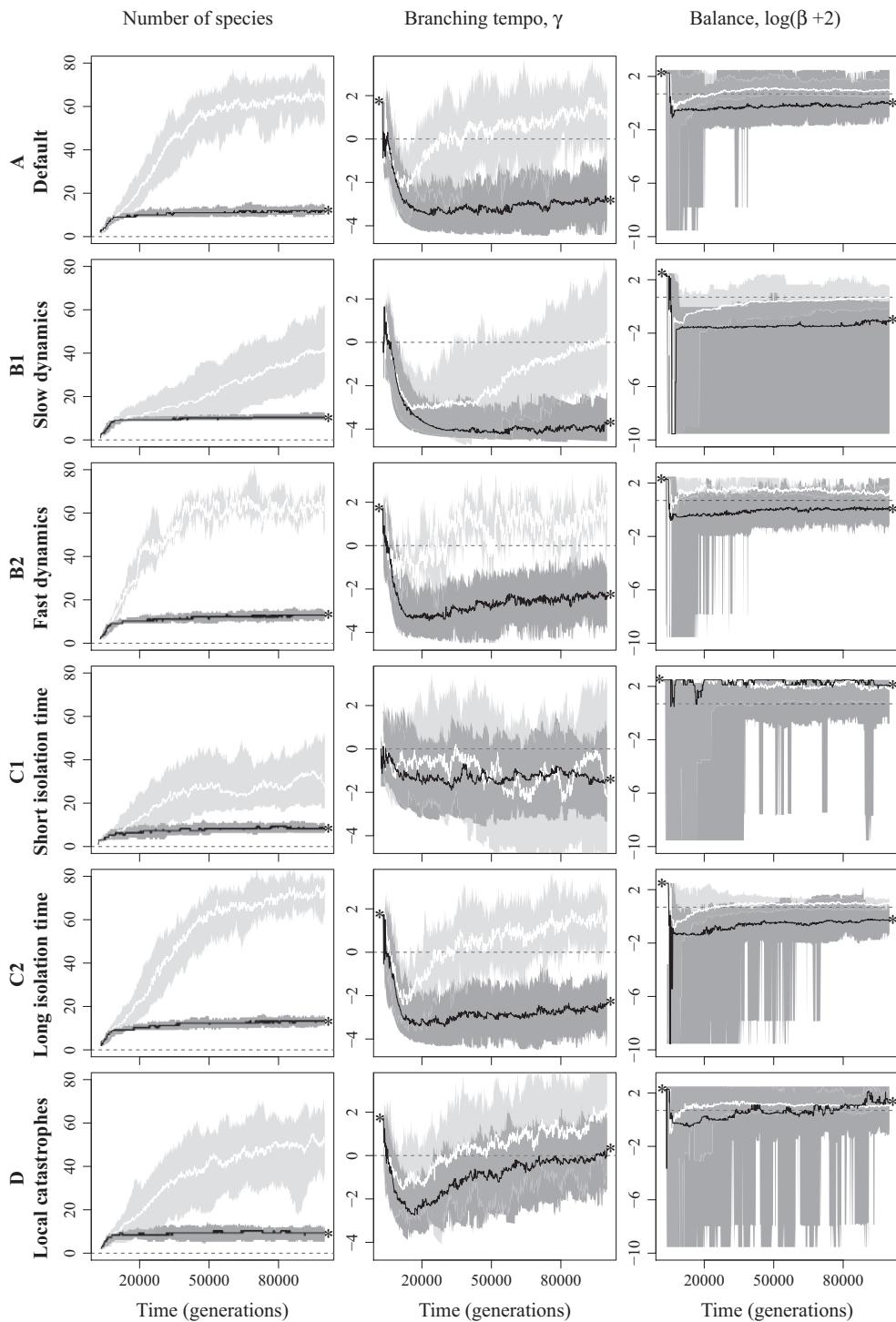


FIGURE 2. Effect of the scaled width of competition and interaction with abiotic factors on the evolution of species diversity, branching tempo γ and balance β of phylogenetic trees as a function of time. Time is measured from the common ancestor's introduction in the landscape. Simulations were replicated 50 times. Black lines give the median (with 95% confidence interval in dark gray) under wide competition ($\sigma_C/\sigma_K = 0.75$); white lines give the median (with 95% confidence interval in light gray) under narrow competition ($\sigma_C/\sigma_K = 0.25$). Stars indicate statistically significant differences (p -value < 0.05) between wide and narrow competition (stars near black lines for differences in median values, t-test; stars on top of dark gray areas, for differences in variance, F-test), either at the beginning or at the end of the simulations (respectively first and last 20,000 generations). Dashed horizontal lines indicate $\gamma=0$ and $\beta=0$. Rows B1 and B2 test for the effect of the pace of landscape dynamics (default A $\approx 4.76 \cdot 10^{-5}$, B1 $\approx 9.9 \cdot 10^{-6}$, and B2 $\approx 9.8 \cdot 10^{-5}$). Rows C1 and C2 test for the effect of time in isolation (default A ≈ 0.95 , C1 ≈ 0.52 , and C2 ≈ 0.99). Row D tests for the effect of local catastrophes (default A = 0 and D = 2.10^{-4}). See Table 1 for other parameter values.

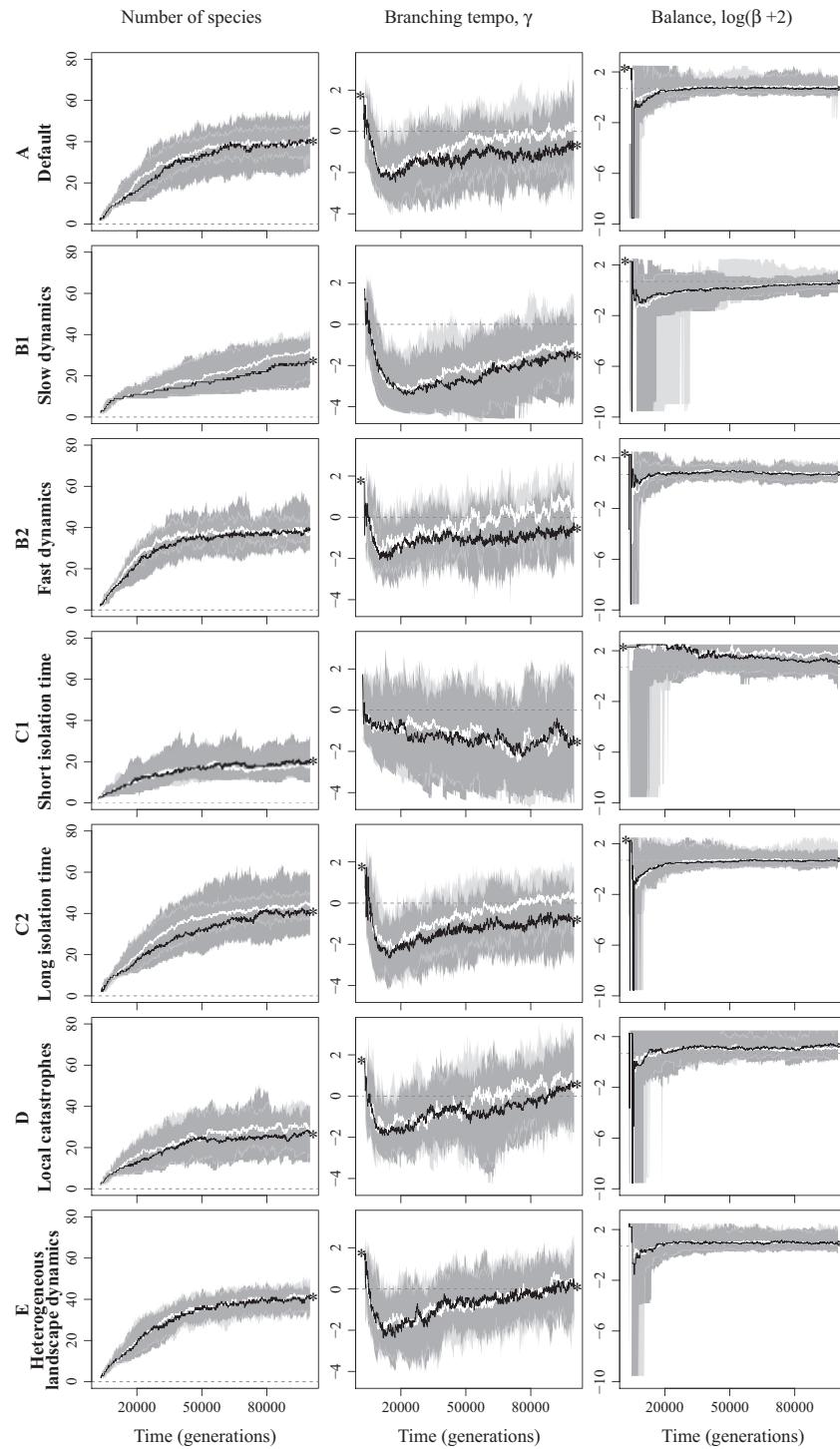


FIGURE 3. Effect of spatial heterogeneity in the scaled width of competition and interaction with abiotic factors on the evolution of species diversity, branching tempo γ and balance β of phylogenetic trees as a function of time. Time is measured from the common ancestor's introduction in the landscape. Simulations were replicated 50 times. Black lines give the median (with 95% confidence intervals in dark gray) with heterogeneity; white lines give the median (with 95% confidence intervals in light gray) without heterogeneity. Stars indicate statistically significant differences (p -value < 0.05) with versus without heterogeneity (stars near black lines for differences in median, t -test; stars on top of dark gray areas for differences in variance, F -test), either at the beginning or at the end of the simulations (respectively first and last 20,000 generations). Dashed horizontal lines indicate $\gamma=0$ and $\beta=0$. Rows B1 and B2 test for the effect of the pace of landscape dynamics (default $A \approx 4.76 \cdot 10^{-5}$, $B1 \approx 9.9 \cdot 10^{-6}$, and $B2 \approx 9.8 \cdot 10^{-5}$). Rows C1 and C2 test for the effect of time in isolation (default $A \approx 0.95$, $C1 \approx 0.52$, and $C2 \approx 0.99$). Row D tests for the effect of local catastrophes (default $A=0$ and $D=2 \cdot 10^{-4}$). Row E shows results when spatial heterogeneity impacts landscape dynamics rather than competition width (heterogeneity intensity ≈ 0.46). See Table 1 for other parameter values.

We studied how the shape of phylogenetic trees is affected by the scaled width of competition, σ_C/σ_K (Doebeli and Dieckmann 2003). The ratio of the standard deviation of the competition kernel, σ_C , over the standard deviation of the maximum carrying capacity per site, σ_K , measures the range of resources utilized by each species relatively to the total range of available resources in each site. It is inversely proportional to the number of available local niches. Under wide (scaled) competition (low σ_K , high σ_C), resources are concentrated close to the ecological optimum while the intensity of competition declines slowly with phenotypic distance, which broadens the range of resources utilized by each species, resulting in fewer available local niches. In contrast, under narrow (scaled) competition (high σ_K , low σ_C), resources are more widely distributed while the intensity of competition declines rapidly with phenotypic distance, which narrows the range of resources utilized by each species, resulting in a higher number of available local niches. We tested values of σ_C/σ_K in {0.25, 0.375, 0.5, 0.75}, using values of σ_C in {0.3, 0.4, 0.5, 0.6} and σ_K in {0.8, 1.0, 1.1, 1.2}.

To investigate how the effect of the scaled width of competition on the shape of phylogenetic trees interacts with abiotic factors, first we looked at the effect of the pace of landscape dynamics (cycles of fusion and fragmentation of adjacent sites), as measured by $1/(1/f + 1/c)$ (with f the rate of border appearance and c the rate of border disappearance). The default pace is $\approx 4.76 \cdot 10^{-5}$ ($f = 10^{-3}$, $c = 5.10^{-5}$; Table 1). Low pace was set to $9.9 \cdot 10^{-6}$ ($f = 10^{-3}$, $c = 10^{-5}$), and fast pace was set to $9.8 \cdot 10^{-5}$ ($f = 5.10^{-3}$, $c = 10^{-4}$). Second, we looked at the effect of the time in isolation, measured by the fraction of time that a border is closed on average, $f/(c+f)$. When the time in isolation is long, the species in adjacent geographical sites tend to spend more time in allopatry, and less time in sympatry. Default, low, and high values of isolation time are 0.95, 0.52, and 0.99, respectively. Third, we looked at the effect of the rate of local catastrophe, cr . We compared the no-local catastrophe scenario ($cr=0$) to a case where the local catastrophe rate is high enough to decrease the species richness at steady state, but low enough to allow diversification ($cr=2.10^{-4}$).

We further investigated the influence of spatial heterogeneity by assuming that each geographical site could have its own values of σ_C and σ_K . In this case, σ_C and σ_K were drawn randomly from {0.3, 0.6} and {0.8, 1.2}, respectively. This allowed us to keep the same average ratio $\sigma_K/\sigma_C=2.5$ over all sites in both the with- and without-heterogeneity simulations (ensuring a similar number of available local niches in the landscape). Here again, we explored how this effect is modulated by abiotic factors (pace of landscape dynamics, time in isolation and local catastrophes), using the same parameter values as above.

Finally, we addressed the effect of spatial heterogeneity in landscape dynamics by randomly assigning to each geographical border a rate of

appearance f , picked in $\{4.10^{-4}, 2.10^{-3}, 4.10^{-3}\}$, and a rate of disappearance c , picked in $\{2.2 \cdot 10^{-5}, 5.10^{-5}, 8.10^{-5}\}$. We compared the resulting tree shapes to those generated without heterogeneity (all borders having $f=10^{-3}$ and $c=5.10^{-5}$). These values ensure the same average pace of landscape dynamics, $4.76 \cdot 10^{-5}$, and the same average time in isolation, 0.95, in both sets of simulations. They also enable us to keep a similar level of spatial heterogeneity in scaled competition width and in landscape dynamics. Indeed, the ratio $\sqrt{\text{var}(\text{pace}_h)/\text{pace}_d}$ of the standard deviation of all the equiprobable values pace_h of pace of landscape dynamics with heterogeneity over pace_d , the default pace without heterogeneity, is equal to the ratio $\sqrt{\text{var}((\sigma_K/\sigma_C)_h)/(\sigma_K/\sigma_C)_d}$ of the standard deviation of all the equiprobable values $(\sigma_K/\sigma_C)_h$ with heterogeneity over $(\sigma_K/\sigma_C)_d$, the default value without heterogeneity.

The model was coded in C language using the GNU Scientific Library (Galassi et al. 2009) for random number generation. Computation and analyses of phylogenetic trees were performed using R (R Development Core Team 2012) and the packages ape (Paradis et al. 2004) and apTreeshape (Bortolussi et al. 2006). Codes are available as a ready-to-use R function, available in the Dryad data repository doi:10.5061/dryad.3bp51.

RESULTS

Phylogenetic Tree Shape Through Time - Example

First, we describe some of the salient features of the phylogenetic trees that come out when the model is run for a specific set of parameter values (Fig. 1). Simulations were replicated over 10^5 generations. Figure 1A shows that species diversity increases smoothly up to a stationary phase, with only small variation among replicates. Rather unexpectedly, the shape of the phylogenetic trees shows more complicated patterns, both across time and among replicates (Fig. 1B,C). Trees of different age, that is, time elapsed between the root and the time at which the 'leaves' are observed, can differ markedly in branching tempo and imbalance. After an initial phase where β is highly unpredictable and γ rapidly peaks then decreases (age class labeled (1) in Fig. 1B,C), trees tend to be stemmy and unbalanced (median $\gamma < 0$, median $\beta < 0$; age class (2)). However, after this initial decrease, β starts increasing, followed by γ from age class (3). In older trees, the topology stabilizes around a stationary state, which under this parameter set tends to be overbalanced (median $\beta > 0$ from age class (4)), with variation among replicates decreasing over time. Meanwhile, γ continues to increase and trees become tippy (median $\gamma > 0$). In the class of oldest trees (age class (5)), the branching tempo of phylogenetic trees also reaches a stationary state.

Five remarks can thus be made on the dynamics of diversification and tree shape for this particular set of parameter values: (i) Combining the ecological

processes of intra- and interspecific local competition with large-scale, stochastic landscape factors does not prevent a smooth buildup and stabilization of species diversity from emerging. (ii) Trees of different ages have different shapes; this is true even among older communities that have reached the diversity plateau. (iii) Deceleration in branching ($\gamma < 0$), which conventional thinking associates with communities that are old enough to be ecologically saturated, is in fact only observed among the young trees (age class (2) in Fig. 1's example, while species diversity is not even close to half the stationary level). (iv) Phylogenetic trees tend to shift from stemmy and unbalanced ($\gamma < 0, \beta < 0$) to tippy and over-balanced ($\gamma > 0, \beta > 0$). (v) Young phylogenetic trees exhibit more among-replicates variability in balance β , but less among-replicates variability in branching tempo γ than old phylogenetic trees.

We can relate these observations to the underlying biotic and abiotic factors of speciation and extinction. Initially, only one ancestral species is present in the landscape, but rapidly an allopatric speciation event occurs at each geographical site across the landscape, due to directional selection toward the ecological optimum (local adaptation). Because most of these speciation events directly originate by sequential differentiation from the ancestral species, young trees tend to be unbalanced. Within this class of young trees, γ tends to be negative because all allopatric speciation events occur within a short-time window (they occur independently and from the same process of directional selection), and much earlier than the next speciation events driven by landscape dynamics. Indeed, landscape dynamics cause speciation only if diverging populations are sufficiently ecologically different and sufficiently choosy for reinforcement at secondary contact to lead to stable sympatric coexistence. Choosiness only begins to evolve after populations have adapted to the local ecological optimum of their geographical site, due to disruptive selection, and independently of landscape dynamics. Therefore, landscape dynamics may cause speciation only after the initial allopatric radiation and evolution of assortative mating.

As trees grow into age class (2), the species formed in allopatry in each site start to split due to landscape dynamics. Because all geographical borders in the landscape have the same rates of appearance and disappearance, these speciation events are homogeneously distributed among lineages, and β starts to increase. The concurrent fact that γ continues to decrease indicates that the most recent speciation events occurring due to landscape dynamics do not occur fast enough to compensate for the increase in length of the branches formed by the allopatric speciations during age class (1). This compensation starts as trees grow into age class (3), when γ then starts to increase. This reflects an increase in species diversity due to landscape dynamics, associated with species turnover. When age class (4) is reached, tree balance β plateaus. In contrast, γ continues to increase until age class (5), and only then stabilizes around a stationary value. At this point in

time the early imbalance and stemminess of the trees have been overwhelmed by subsequent diversification due to landscape dynamics and by turnover due to competition and demographic stochasticity. Moreover, the proportion of species that originated from the early allopatric radiation has been strongly reduced, and so has their influence on the shape of phylogenetic trees.

The above processes of diversification are also responsible for the increase in variance of γ and the decrease in variance of β among simulation replicates over time. First, young phylogenetic trees have lower variance in γ than older ones because allopatric speciation events generate less variability in branching tempo than diversification due to landscape dynamics: The early allopatric radiation develops similarly in all simulation replicates, whereas landscape dynamics depend on random variation in the number and distribution of removal of geographical barriers. Second, young phylogenetic trees have higher variance in β than older ones because they contain fewer species (online Appendix 7 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>, showing the relationship between species richness and variance in β in phylogenetic trees simulated under the birth-death model).

Effect of Ecological Processes - Competition Width

Figure 2A illustrates the effect of the scaled width of competition on the shape of phylogenetic trees of different age. The scaled width of competition is measured by the ratio σ_C/σ_K of the width of the competition kernel over that of the carrying capacity function. It is negatively related to the number of local ecological niches in the stationary state of the metacommunity composition. Patterns obtained under narrow versus wide competition are shown in light versus dark gray.

Increasing the scaled width of competition results in lowering both γ and β values and keeping them negative over a wider range of tree age; γ and β may even remain negative at all tree ages, as in the wide competition regime shown in Figure 2A. Under narrow competition, the number of local ecological niches is high, and thus many speciation events occur due to landscape dynamics, driving γ and β toward positive values. This pattern is reinforced by the large number of species and their ecological similarity at steady state, which increase the actual effects of competition and raise species turnover. Under wide competition, the number of local ecological niches is low, diversity is more limited, and thus few speciation events occur due to landscape dynamics. As a consequence, γ and β tend to retain the footprint of the initial allopatric radiation and to remain negative. This pattern is reinforced by the small number of species at steady state and their large ecological differentiation, which reduces the intensity of competition and hence reduces the species turnover.

Furthermore, increasing the scaled width of competition affects the variability of branching tempo γ and balance β . On the one hand, wide competition increases the variance in β among simulation replicates (Fig. 2A, with VT=2.30, VS=3.96 under narrow competition, and VT=2.54, VS=8.24 under wide competition). Wide competition indeed limits species diversity, increasing variance in β due to stochasticity (Fig. 1, online Appendix 7 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>). On the other hand, wide competition decreases the variance in γ , both through time and among replicates (Fig. 2A, with VT=1.21, VS=1.30 under narrow competition, and VT=0.46, VS=0.58 under wide competition). Under wide competition, most branching events result from the initial allopatric radiation, which generates less variability in γ than diversification due to landscape dynamics (Fig. 1).

How Abiotic Factors Interact with Competition

Pace of landscape dynamics.—The effect of competition on the shape of phylogenetic trees is not altered by the pace of landscape dynamics. Figure 2A,B1,B2 show that at either slow or fast pace, wide competition always decreases γ and β by a similar amplitude. Under both wide and narrow competition, the pace of landscape dynamics essentially scales the effect of tree age on β and γ : fast landscape dynamics promote a rapid increase in γ and β following the allopatric radiation, and increase their stationary values. This is because landscape dynamics drive diversification after the initial allopatric radiation (Aguilée et al. 2013); when fast, they obliterate the influence of the allopatric radiation (negative γ and negative β) on phylogenetic tree shape.

However, the pace of landscape dynamics influences how the scaled width of competition affects the variance in γ and β . First, slow landscape dynamics amplify the increase in the variance of β under wide competition. This effect is likely related to the relationship between species richness and variance in β (online Appendix 7 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>). Second, both slow and fast dynamics amplify the difference in the variance of γ under narrow and wide competition, but in different ways: slow landscape dynamics reduce the variance in γ under wide competition, whereas fast landscape dynamics reduce the variance in γ under narrow competition. This results from three different effects acting on the variance in γ : the importance of landscape dynamics compared to that of the initial allopatric radiation (which increases the variance in γ under narrow competition and fast dynamics), the stochasticity in the location of the branching events within small phylogenetic trees (which increases the variance in γ under wide competition and slow dynamics), and the stochasticity of landscape dynamics (which increases the variance in γ under slow dynamics).

Time in isolation.—Inspecting Fig. 2A,C1,C2 shows that isolation time strongly interacts with competition to shape phylogenetic trees. Short isolation time reduces the effect of variation in scaled competition width. Indeed, short isolation time causes populations to spend less time in allopatry, which limits their potential to differentiate, hence decreases the likelihood of speciation and increases the chance of hybridization and the risk of extinction in sympatry. As a consequence, both the initial allopatric radiation and the subsequent diversification due to landscape dynamics occur more slowly, and species diversity at steady state is lower.

This has two consequences for phylogenetic tree shape. First, species take more time to evolve assortative mating and thus many initial species can originate from one another sequentially (rather than from the ancestral species). This yields phylogenetic trees that are balanced under both narrow and wide competition. Second, the initial allopatric radiation is now temporally overlapped by the subsequent diversification due to landscape dynamics, and the species diversity resulting from landscape dynamics is lower at steady state. Consequently, temporal variation in branching tempo is much less pronounced and phylogenetic trees are buffered against the strong influence of competition width.

Overall, these results underscore the importance of geographical isolation for the ecological effects of competition to manifest themselves. Lasting isolation favors diversification while allowing ecological interactions (competition) to exert a strong, negative influence over the number of species at stationary metacommunity composition.

Local catastrophes.—Frequent local catastrophes decrease the effect of the scaled width of competition on both branching tempo γ and balance β (Fig. 2A,D). When the rate of local catastrophes is high, branching tempo under wide competition becomes close to its value under narrow competition. Wide competition yields a large proportion of old lineages (formed during the early allopatric radiation), of which many are removed by local extinctions; as this happens, ecological niches open for new species to arise. The average age of the nodes in the phylogenies decreases as a consequence, which translates into an increasing branching tempo γ . These effects do not manifest under narrow competition because most species are recent, and thus most species impacted by local extinctions are also recent.

Local catastrophes also increase tree balance β under wide competition, reducing the difference with its value obtained under narrow competition (Fig. 2A,D). Indeed, local extinctions cause the loss of old lineages that originated from the same ancestral species, which in turn permits the evolution of more recent species more homogeneously spread among the different subclades. Moreover, the decrease in species richness (e.g., median value going from about 12 to 9 under wide competition, and from 62 to 51 under narrow competition, in Fig. 2A,D) may increase median β , as

expected under the birth–death model (online Appendix 7 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>).

Eventually, local catastrophes increase β variability. On the one hand, their random occurrence in time and space generates stochastic effects on tree shape. On the other hand, they cause an overall decline in species richness – an effect that in itself causes more variability in β under the birth–death model (online Appendix 7 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>).

Spatial Heterogeneity

Overall, spatial heterogeneity in scaled width of competition (i.e., different competition widths among geographical sites) has little qualitative effect on the patterns of branching tempo γ and imbalance β – even though quantitative differences tested in the oldest trees are all significant (Fig. 3A). Although heterogeneity in competition width has virtually no effect on the dynamics of species richness, it tends to delay the stabilization of γ and, to a lower extent, β . As a consequence, the value of γ may switch sign from positive to negative in old trees.

These results cannot be explained by differences in the total number of available local niches in the landscape with and without heterogeneity because our simulations control for a constant $\sigma_K/\sigma_C = 2.5$ across the landscape in both scenarios. However, plotting the stationary values of γ as a function of the scaled width of competition σ_C/σ_K without heterogeneity helps understand this effect (online Appendix 8 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>): the rate of decrease in γ increases non linearly with competition width, which suggests that in the presence of spatial heterogeneity, γ may be driven downward by geographical sites in which competition is wider.

The influence of spatial heterogeneity on the branching tempo of phylogenetic trees is amplified by fast landscape dynamics and long isolation time, but prevented by slow landscape dynamics, short isolation time, or the frequent occurrence of local catastrophes (Fig. 3A–D). The latter are abiotic conditions that indeed limit species diversification or species diversity at steady state, reducing the influence of competition width on phylogenetic tree shape, and thus that of spatial heterogeneity in competition width.

We also examined the effect of spatial heterogeneity in landscape dynamics (Fig. 3E), which also causes both γ and β to decrease, but to a lower extent than spatial heterogeneity in scaled competition width. Species close to slowly changing geographical borders tend to diversify less rapidly than species close to borders which undergo fast dynamics, reducing the balance and branching tempo in phylogenetic trees. However, this effect on the process of diversification is limited, and is

smaller than that of spatial heterogeneity in competition width, which determines the distribution of species in geographical sites at steady state.

DISCUSSION

We have reported on the shapes of phylogenetic trees generated by an individual-based model of adaptive radiation driven by ecological speciation in a dynamic landscape. Our model is likely to apply to a broad range of real diversification histories. Macroevolution often proceeds in bouts of radiations, and landscape dynamics are likely to have played a role in many (Schluter 2000). Celebrated examples include the radiation of the cichlid fishes in the Great African Lakes (Sturmbauer 1998; Schwarzer et al. 2012; Aguilée et al. 2013), groups of plants and insects in the Macaronesian islands (Rijstdijk et al. 2014), and certain clades of birds in Amazonian forests (Haffer 1969; Terborgh 1992; Haffer 1997; Hill and Hill 2001; Weir 2006; Sedano and Burns 2010). However, phylogenetic tree shape is expected to depend on key features of the diversification process. Pigot et al. (2010) and Davies et al. (2011) showed that vicariance associated with high range expansion, or peripatric speciation producing many species of lower abundance, can generate unbalanced phylogenetic trees by causing strong asymmetry in population size at speciation. Pontarp et al. (2012) highlighted that when within-site disruptive selection occurs before between-site directional selection, phylogenetic trees are more balanced and the deceleration in branching is less pronounced. Similarly, frequent sympatric speciation (Dieckmann and Doebeli 1999), recurrent allopatric speciation following successive landscape fragmentation events (Pigot et al. 2010), or sexual selection (e.g., Darwin 1871; Barraclough et al. 1995; Mitra et al. 1996) may all influence phylogenetic tree shape.

Dependence of Phylogenetic Tree Shape on Clade Age

Our results show that the tree shape is expected to change as a clade ages. This temporal pattern of variation results from the combination of two different mechanisms of diversification. First, species differentiate under directional selection as they adapt locally to different ecological optima. This is the classical scenario of adaptive radiation (Schluter 2000). Because these speciation events occur at fairly similar rates across lineages and before the evolution of assortative mating, and because most of the derived species originate from the same ancestral species, phylogenetic trees initially exhibit decelerating branching and imbalance ($\gamma < 0$ and $\beta < 0$). Second, these species may further differentiate due to cycles of directional selection and reinforcement caused by the dynamics of the abiotic environment. This process is germane to the “species pump” mechanism (Greenwood 1965; Rossiter 1995; Aguilée et al. 2013). The new speciation events are homogenously

distributed among subclades and occur sequentially, thus generating an increase in branching tempo γ and balance β , potentially reaching positive values.

In our model, the early phase of diversification, and corresponding tree shape, is influenced by the site of introduction of the ancestral species. Introduction in a peripheral site causes border effect, resulting in less temporal variation in species tree shape, and a tendency for trees to be more balanced (online Appendix 5 available as Supplementary material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>).

Whereas the clade age-dependence of β may not have been, to our knowledge, recognized or even hypothesized in earlier studies, previous studies have already considered or built hypotheses around the variation in branching tempo with clade age (e.g., MacArthur 1972; Rosenzweig 1978; Pimm 1979; Walker and Valentine 1984; Nee et al. 1992; Lovette and Bermingham 1999; Weir 2006; McPeek 2008; Phillimore and Price 2008; Liow et al. 2010; Jönsson et al. 2012). The conventional view is that young and still diversifying clades should exhibit phylogenetic trees with positive branching tempo, whereas ecological saturation due to competition should result in negative branching tempo. Accordingly, McPeek (2008) found that slow-trait evolution opposing ecological niche filling results in positive γ values, whereas fast-trait evolution leading to ecological niche filling results in negative γ values. This view was challenged by Liow et al. (2010): their diversity-dependent lineage-based model with significant extinction predicted negative γ in young clades and positive γ in older ones. This pattern is similar to our findings (Fig. 1B), and results from diversity dependence associated with species turnover, which erodes the footprint of initial radiation and increases the number of recent nodes in older clades. However, unlike Liow et al. (2010), our model uncovers a diverse array of quantitative effects of competition and abiotic factors on γ , which may eventually result in either positive or negative γ in old clades (Figs. 2 and 3).

Our results confirm that the speed of convergence toward the stationary metacommunity size differs from that toward the stationary branching tempo of phylogenetic trees, and from that toward their stationary balance (e.g., Figs. 2A,B2 and 3A,B2,C1, Liow et al. 2010). Thus, negative or positive γ values should not be taken as revealing an actual decrease or increase in the diversification rate through time. They may be strongly related to early variation in the diversification rate as well as to temporal changes in the rate of species turnover. This clearly illustrates (McPeek's 2008) cautionary note that γ only quantifies the overall variation (since the root) in the rate of lineage accumulation in reconstructed phylogenies.

Effects of Competition Width

Similarly to McPeek (2008), we found that taking the ecological context of speciation and extinction into account is critical to understand patterns of phylogenetic

tree shape. A major difference of our model from McPeek (2008) is that we not only considered the intensity of ecological differentiation at speciation events, but also accounted for sustained competition among organisms. This allowed us to study not only the effect of ecological niche filling (as in McPeek 2008, but with different results - see previous paragraph), but also the effect of competition all along the metacommunity's history.

Our results show that under wide competition (wide competition kernel and narrow distribution of resources), the branching tempo and balance of phylogenetic trees are determined primarily by the initial allopatric radiation: in the long run, they keep a decelerating branching tempo and remain unbalanced ($\gamma < 0$ and $\beta < 0$). In contrast, under narrow competition (narrow competition kernel and wide distribution of resources), the shape of phylogenetic trees evolves rapidly: at steady state, trees are overbalanced, with positive branching tempo ($\beta > 0$ and $\gamma > 0$). Thus, no simple causal relationship should be expected between ecological niche filling and branching deceleration.

These results generate some predictions similar to McPeek (2008). Clades with negative γ (young clades, and old clades evolving under wide competition) should harbor species that are ecologically well differentiated and exhibit little overlap of their geographic range. Clades with positive γ (old clades evolving under narrow competition) should contain species that are poorly differentiated, with substantial overlap in their geographic range.

Another implication of these results is that negative γ values are not necessarily associated with zero-extinction rates. Some earlier theoretical studies argued that negative γ could only be generated under zero-extinction rates (e.g., Weir 2006; Rabosky and Lovette 2008b), a conclusion that was difficult to reconcile with data from the fossil record (e.g., Stanley 1979; Raup 1991; Gilinsky 1994; Alroy 1996; Foote 2000). Our results yield a more nuanced prediction: negative γ occurs under biotic or abiotic conditions which are conducive to extinction rates at steady state that are low but non-zero (e.g. under wide competition - Fig. 1, short isolation time - Figs. 2C1 and 3C1, or spatial heterogeneity - Fig. 3A,E).

Finally, our results uncover the important influence of the width of competition on tree balance, β (Fig. 2A). By controlling the magnitude of diversification due to landscape dynamics, competition width determines to what extent phylogenetic tree shape depends on early history (dominated by the allopatric radiation; wide competition) versus late history (driven by landscape dynamics; narrow competition) of diversification.

Effects of spatial Heterogeneity

Spatial heterogeneity, either in scaled width of competition or in rates of landscape dynamics, can decrease the balance of phylogenetic trees (Fig. 3A-D). Spatial heterogeneity in competition width generates differences among geographical sites in the

number of species that can coexist at steady state. Spatial heterogeneity in landscape dynamics generates differences among subclades in the propensity to diversify. These effects, however, are fairly small, and do not generate the degree of imbalance seen in real reconstructed phylogenies (e.g., Guyer and Slowinski 1991; Heard 1992; Guyer and Slowinski 1993; Slowinski and Guyer 1993; Mooers 1995; Purvis 1996; Mooers and Heard 1997; Blum and François 2006). This may be due to the limits that our model sets on spatial heterogeneity (i.e., low variance of σ_C/σ_K and pace of border dynamics across the landscape), and space subdivision (only 9 distinct sites).

In the wild, spatial heterogeneity is likely to be the rule at all spatial scales, both in ecological interactions and environmental dynamics. Therefore, we expect spatial heterogeneity in both to contribute significantly to real phylogenetic tree imbalance, in line with previous claims (e.g., Simpson 1944; Rosenzweig 1995; De Queiroz 2002; Purvis et al. 2011). For example, in birds Owens et al. (1999) showed that clade size is associated with feeding habits and dispersal abilities: at higher taxonomic level, heterogeneity in feeding habits and dispersal abilities among clades is, therefore, expected to generate imbalanced phylogenetic trees. Such effects might be enhanced further by temporal heterogeneity in biotic and abiotic features (e.g., Grant 2003).

Interestingly, spatial heterogeneity in competition and landscape dynamics also slows down branching, by preventing diversification in sites that experience wide competition or have boundaries that rarely open. Ubiquitous natural heterogeneity of ecological systems is, therefore, expected to result in branching slowdown in real phylogenetic trees.

Modulation by Abiotic Factors

Our results show that the influence of ecology on macroevolutionary patterns is modulated by abiotic factors. Yet, different abiotic factors interact differently with ecological factors to influence phylogenetic tree shape. The effect of the scaled width of competition on tree shape is almost unaltered by the pace of landscape dynamics. Even though the latter controls the potential rate of diversification after the initial allopatric radiation, and therefore influences tree shape, its effect is largely independent of that of competition width. Landscape dynamics present the metacommunity with opportunities for diversification; ecological interactions (competition) determine the successes and failures of the diversification process.

Both the time spent in isolation and the occurrence of local catastrophic extinctions can almost obliterate the relationship between competition and phylogenetic tree shape. Short isolation time decreases the rate of lineage accumulation and limits species richness in metacommunity stationary state, thus hampering ecological niche filling. Local catastrophic extinctions remove species produced by ancient branching events, thus promoting new speciation events driven by

landscape dynamics and again limiting ecological niche filling. Both processes thus erase the footprint of early history and strengthen the recent history in phylogenetic trees, as anticipated by Haydon et al. (1994).

Ecology and the Shape of Real Reconstructed Phylogenies

To generate hypotheses on the mechanisms that could be responsible for branching slowdown (e.g., Nee et al. 1992; Zink and Slowinski 1995; Lovette and Bermingham 1999; Rüber and Zardoya 2005; Seehausen 2006; Weir 2006; McPeek 2008; Rabosky and Lovette 2008a; Jönsson et al. 2012) and imbalance (e.g., Guyer and Slowinski 1991, 1993; Mooers 1995; Purvis 1996; Mooers and Heard 1997; Blum and François 2006) in most real phylogenies (see also online Appendix 9 available as Supplementary Material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>), we examined the conditions, in terms of clade age, competition width, spatial heterogeneity, and abiotic conditions, under which our model predicts negative versus positive γ and β (Figs. 2 and 3). It turns out that young phylogenetic trees all tend to exhibit $\gamma < 0$ and $\beta < 0$, except those generated under short isolation time. In old clades, at least two mechanisms may keep β and γ at negative values: wide competition preventing further diversification, and spatial heterogeneity. These negative γ and β values in old trees are, however, only obtained under low rates of local catastrophes, and a sufficiently long time in isolation.

These results provide new insights on how to interpret β and γ from real phylogenies. First, negative γ should not necessarily be interpreted as evidence for ecological niche filling or wide competition: γ is negative in young trees under narrow competition, and in trees of any age under any competition width provided the time in isolation is short. Similarly, positive γ is not necessarily related to early steps of diversification or to narrow competition: γ is positive in trees of old clades evolving under wide competition if frequent local catastrophes occur. Second, negative β does not necessarily reflect spatial heterogeneity: β is negative without spatial heterogeneity if trees are young, or if competition is wide. Similarly, positive β does not necessarily depend on the landscape homogeneity: β is positive in the presence of spatial heterogeneity if the time in isolation is short.

Pigot et al. (2010) argued that their geographic model of species' birth and death predicts a pattern of phylogenetic imbalance correlating with decelerating branching. We also found a tendency toward a correlation between the signs of median γ and median β (Figs. 2 and 3). This is due to three different processes affecting γ and β in the same direction: the initial allopatric radiation (which decreases both γ and β), diversification driven by landscape dynamics (which increases both γ and β), and spatial heterogeneity (which decreases both γ and β). However, as highlighted above, the correlation does not always hold: it varies with clade age and may be prevented by abiotic

factors. Interestingly, short isolation time yields a unique combination of median $\gamma < 0$ and median $\beta > 0$, which is not very sensitive to clade age, competition width, or spatial heterogeneity.

Unlike real metacommunities, our simulations include species with very small population sizes (on the order of 100 individuals per species). In larger populations, the rate of speciation is expected to be higher during the phase of diversification (i.e., before the steady state in species richness), due to faster phenotypic divergence. However, at steady state the species turnover should be lower, due to reduced demographic stochasticity. Across wider geographical space, in which the number of available local ecological niches is similar but populations are larger, we therefore expect fewer recent species, especially under narrow competition, and therefore both γ and β might be lower than in our simulations. However, the interaction of competition width and landscape dynamics will still determine the dynamics of diversification. Given the underlying mechanisms as we have understood them from this study, we do not expect qualitative change in the effects of competition width and landscape dynamics on phylogenetic tree shape.

Eventually, our simulations show high variability in γ and β through time and among replicates, in agreement with the analysis of real phylogenies (e.g., Purvis 1995; Pybus and Harvey 2000; Barraclough and Vogler 2002; Linder et al. 2003; Turgeon et al. 2005, and online Appendix 9 available as Supplementary Material on Dryad at <http://dx.doi.org/10.5061/dryad.3bp51>). This variability originates from the intrinsic stochasticity of the diversification process, and is amplified by small species numbers. As a result, global patterns of variation in γ and β may hint at important processes, but individual values for particular clades may be difficult to interpret: two clades may exhibit quite different values of γ and β even though they evolved under similar biotic and abiotic conditions.

Generalizing the Use of Individual-Based Models of Species Diversification

Our model (in open access in the Dryad data repository at <http://dx.doi.org/10.5061/dryad.3bp51>) is easy to modify and run to test for the effect of other factors or processes on phylogenetic tree shape, such as the mating system (role of sexual selection), the landscape structure and dynamics, ecological optima that fluctuate over time, key innovations, the structure of correlations among ecological traits, and interspecific ecological processes beyond symmetrical competition (e.g., asymmetric competition, consumer-resource interactions, mutualism, or parasitism). Our modeling framework indeed mostly applies to phylogenetic trees documented at the scale of genera, at which all species are more likely to share the same trophic level, and to interact through interspecific competition for resources. As more phylogenies become available at higher

taxonomic levels and among ecologically connected groups, such extensions will be particularly relevant.

Individual-based models of species diversification should allow investigation of a wide range of questions in macroevolutionary biology. They allow researchers to integrate biotic and abiotic processes across multiple scales, from the genetic determination of individuals' traits to large-scale environmental changes, and to study the complete history of diversification by speciation and extinction. This should help build the theory needed to fill the gap between paleoenvironmental data, the fossil record, and phylogenetic trees reconstructed from extant molecular sequences.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3bp51>.

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