



SPECIAL
PAPER



The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity

Mikael Pontarp^{1,2,*} and John J. Wiens³

¹Department of Evolutionary Ecology, Lund University, SE-223 62 Lund, Sweden,

²Institute of Evolutionary Biology and Environmental Studies, University of Zurich, 8057 Zurich, Switzerland, ³Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721-0088, USA

ABSTRACT

Aims Patterns of species richness, such as the remarkable biodiversity of tropical regions, have been documented and studied for centuries. However, their underlying evolutionary and ecological causes are still incompletely understood. A commonly stated paradigm in the literature is that high richness in some habitats is directly caused by one of three competing explanations: (1) greater time-for-speciation (earlier colonization), (2) more rapid diversification rates (faster speciation relative to extinction) or (3) higher carrying capacity. However, these three explanations have been relatively little studied using theoretical approaches (especially in terms of comparing all three). Furthermore, empirical studies give conflicting results about their relative importance. Here, we use simulations to study the processes that drive richness patterns along environmental gradients.

Location Globally applicable.

Methods We use individual-based and trait-based modelling of eco-evolutionary dynamics to simulate the evolutionary radiation of a clade across five habitats with differing ecological conditions, and track patterns of species richness within and between habitats over time. We specifically address the roles of time and diversification rates in explaining richness patterns and the potential impact of carrying capacity.

Main results and conclusions Contrary to the widespread paradigm, we find that variation in carrying capacity can underlie differences in diversification rates and time-for-speciation among habitats. Therefore, carrying capacity is not a competing, alternative explanation for richness patterns. We also find that the time-for-speciation effect dominates richness patterns over short time-scales, whereas diversification rates dominate over longer time-scales. These latter observations can help reconcile the seemingly conflicting results of many empirical studies, which find that some patterns are explained by time and others by differences in diversification rates.

Keywords

carrying capacity, competition, dispersal, diversification, niche, simulation, speciation, species richness, time-for-speciation

*Correspondence: Mikael Pontarp
Institute of Evolutionary Biology and
Environmental Studies, University of Zurich,
8057 Zurich, Switzerland
E-mail: mikael.pontarp@biol.lu.se

INTRODUCTION

Explaining patterns of species richness is a fundamental goal of biogeography, ecology and evolutionary biology. Species richness often varies along environmental gradients, and at many different spatial scales. For example, many clades have more species in tropical than temperate regions (e.g. Pianka,

1966; Rohde, 1992; Hillebrand, 2004). Yet, richness can also vary among habitats within a region, such as at different elevations (e.g. Rahbek, 1995).

There has been growing appreciation of the idea that these diverse species richness patterns originate through a combination of both ecological and evolutionary processes (e.g. Ricklefs, 1987; Wiens & Donoghue, 2004; Mittelbach *et al.*,

2007). Richness patterns arise through the processes of speciation, extinction and dispersal, where dispersal refers to successful establishment of a lineage in a new region or habitat. These are the processes that directly change the number of species in a given location, even if there is a perfect relationship between richness and one or more environmental variables (i.e. correlations with ecological variables do not negate the importance of these evolutionary and biogeographical processes). Therefore, in order to understand how richness patterns originate along environmental gradients, we need to understand how environmental variables influence these three processes (e.g. Ricklefs, 1987; Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007).

Given this perspective, a widespread paradigm in the literature is that there are three main explanations for why species richness patterns vary along environmental gradients. These explanations involve variation in diversification rates, time and carrying capacity (review in Mittelbach *et al.*, 2007; see also Rabosky, 2009). Many prominent studies have specifically emphasized the idea that these are three competing explanations (e.g. Rabosky & Glor, 2010), especially diversification rates and carrying capacity (e.g. Rabosky, 2009).

First, local environmental conditions at one end of the gradient may increase diversification rates there (diversification is the balance of speciation and extinction over time). Various ecological factors may act to modify these rates and patterns of speciation and extinction (review in Mittelbach *et al.*, 2007). For example, the latitudinal diversity gradient may arise due to higher tropical speciation rates (possibly related to narrower ecological niches in the tropics) and higher temperate extinction rates (potentially caused by climatic changes associated with glacial cycles).

Second, patterns of richness may be explained by the time-for-speciation effect (*sensu* Stephens & Wiens, 2003). Specifically, if one part of the gradient is colonized first, then these habitats may have higher richness simply because there is more time-for-speciation to occur and for species to accumulate in these habitats. Limited dispersal between habitats is a key component of this hypothesis, and may be related to strong ecological differences between habitats and the limited ability of species to adapt to these differences (e.g. niche conservatism; review in Wiens *et al.*, 2010).

Empirical studies have found mixed support for these first two hypotheses, with many studies within regions supporting the time effect (e.g. Brown *et al.*, 2000; Rangel *et al.*, 2007; Wiens *et al.*, 2007; Kozak & Wiens, 2010; Hutter *et al.*, 2013), many larger-scale studies supporting the diversification rate hypothesis (e.g. Jansson & Davies, 2008; Condamine *et al.*, 2012; Pyron & Wiens, 2013; Rolland *et al.*, 2014), and some global-scale studies supporting the time hypothesis within smaller clades (e.g. families: Stephens & Wiens, 2003; Stevens, 2006; Wiens *et al.*, 2006, 2009, 2011; Kozak & Wiens, 2012; Jansson *et al.*, 2013). The explanation for these conflicting results remains unclear.

A third explanation is based on carrying capacity or 'ecological limits' related to finite resources (e.g. Mittelbach

et al., 2007; Rabosky, 2009; but with many earlier antecedents in the ecological and paleontological literatures; e.g. MacArthur & Wilson, 1967; Raup, 1972). This hypothesis is based on the idea that competition for limited resources will constrain the number of species that can occur together in a given location or habitat. However, the specific mechanisms that relate this hypothesis to richness patterns along environmental gradients are still not fully understood. Furthermore, carrying capacity might instead be seen as another ecological factor that influences speciation, extinction and colonization of new habitats over time (Wiens, 2011). Thus, carrying capacity might influence both diversification and time-for-speciation rather than being a third, separate explanation (Wiens, 2011). This makes it difficult to assess the extent to which empirical studies have (or have not) supported this hypothesis.

Despite many empirical studies, the evolutionary and ecological processes that generate richness patterns along environmental gradients remain incompletely understood from a theoretical perspective (i.e. including analytical, modelling and simulation studies). For example, no theoretical studies have addressed under what conditions the time-for-speciation effect might explain richness patterns instead of diversification rates (and thus the reasons for the conflicting results of empirical studies over these two hypotheses are uncertain). Similarly, despite interest in the idea of ecological limits on richness (e.g. Mittelbach *et al.*, 2007; Rabosky, 2009; Rabosky & Glor, 2010), the mechanisms underlying this hypothesis are also unclear (but see Hurlbert & Stegen, 2014). Nevertheless, some theoretical papers have addressed related issues. For example, Goldberg *et al.* (2005) studied how differences in richness develop between two regions, and Roy & Goldberg (2007) examined modelling methods to explain differences in richness between habitats. However, these two studies did not explicitly address the processes underlying richness differences. McPeck (2008) analysed diversification and community assembly along an environmental gradient, but focused on declining diversification rates over time, rather than richness patterns. Birand *et al.* (2012) examined speciation, extinction and range sizes, but not species richness. Stegen *et al.* (2009, 2012a,b) examined how diversity evolves along a temperature gradient, focusing on how temperature impacts diversification and the metabolic theory of ecology (see also Allen *et al.*, 2002). Rosindell & Phillimore (2011) examined the processes underlying richness patterns on islands, but without including ecological differences among islands or species. Rabosky (2012) simulated the time-for-speciation effect, primarily to test the effectiveness of methods for detecting this pattern. Hurlbert & Stegen (2014) examined the possible role of energetic constraints in generating richness patterns, focusing mostly on how the presence of ecological limits influenced patterns of species richness (rather than on the processes by which this occurred). An important set of studies has also used simulations to help address the origins of specific observed richness patterns (review in Gotelli *et al.*, 2009), but have not focused

on the three hypotheses described above. In general, there is an extensive literature on richness patterns (much of which is theoretical; e.g. Hubbell, 2001) but which has not focused on comparing the relative importance of time, diversification rates and carrying capacity. Thus, despite these important contributions, many questions remain unexplored.

Here, we focus on the question of how patterns of species richness arise along environmental gradients. We use individual-based modelling of eco-evolutionary dynamics to simulate the evolutionary radiation of a clade across five habitats with differing ecological conditions (in terms of both abiotic environment and biotic resources), and track patterns of species richness within and between habitats over time. We specifically address the roles of time and diversification rates in explaining richness patterns and the potential impact of carrying capacity. We explore how relevant parameters (e.g. biotic and abiotic niche widths of species, carrying capacity, abiotic and biotic differences among habitats) are related to the processes that directly control richness (speciation, extinction, colonization) and to the build-up of richness among habitats over time. Although simulations cannot match the complexity of real systems, they can offer mechanistic insights that would be difficult to obtain with empirical data alone (e.g. how processes underlie patterns).

We test the following predictions. (1) Following from the carrying capacity hypothesis, overall richness will be positively related to ecological variables increasing resource availability (i.e. narrower resource specialization and higher environmental carrying capacity in some habitats). But this increased richness will be directly caused by influencing diversification rates or the timing of colonization of different habitats. (2) Strong richness gradients will develop rapidly when the first habitat colonized has conditions that potentially promote diversification, such that the effects of time and diversification rates on richness are concordant. (3) In contrast, the differing impacts of diversification rates and time will be most evident when a clade initially colonizes habitats that yield low diversification rates. Under these conditions, species richness should initially be highest in the habitats colonized first (supporting time) but should eventually become highest in habitats that promote diversification (supporting the diversification rates hypothesis). This latter prediction (if supported) might explain why many studies at smaller and shorter spatial and temporal scales support the importance of time (e.g. younger clades), whereas larger scale studies support diversification rates instead.

In the methods section, we describe the details of our model and simulations. We give a brief outline here (Fig. 1). We expand the model by Pontarp *et al.* (2015) to multiple traits and we simulate the evolutionary radiation of a clade over time (starting from a single species) across five habitats that potentially differ in abiotic environments and biotic resources. There is spatial structure among the five habitats but not within them (i.e. all individuals in a habitat can compete). Habitats can be inhabited only by individuals having certain abiotic tolerances and certain values for a trait

that allows them to utilize the biotic resources present in that habitat. These abiotic tolerances and resource-utilization traits can evolve over time (e.g. due to mutation, changes in fitness and selection). Speciation occurs largely through ecological divergence among individuals (Fig. 2), both within and between habitats, and trait-based competition for finite biotic resources is one of the potential drivers of speciation. We also explore the impacts of incorporating non-ecological speciation. Species richness builds up in local habitats over time both through speciation and dispersal among habitats. We explore how overall richness across all five habitats is influenced by changing relevant parameters (e.g. biotic and abiotic niche widths of species, carrying capacity, abiotic and biotic differences among habitats). We then explore how these parameters are related to processes that directly control richness (speciation, extinction, diversification, colonization, and colonization times). Finally, and most importantly, we explore how varying key parameters across habitats influences the build-up of richness among habitats over time.

METHODS

Model outline and general assumptions

We model five discrete habitats along an environmental gradient, each having a specific biotic resource distribution (e.g. seeds of different size for a granivorous bird) and values for an abiotic environmental variable (e.g. temperature). Individuals are defined by their resource utilization trait and an abiotic tolerance trait. Resources in each habitat are modelled as a Gaussian resource distribution (see equation 2 below) in trait dimension (z) and a population of identical individuals will have a local carrying capacity based on its utilization trait (also in trait dimension z) (Fig. 2). Continuing with the seed/bird analogy, a habitat with relatively few small and large seeds but many intermediate-sized seeds, and a bird population with intermediate-sized beaks will therefore have a larger carrying capacity in that habitat than birds with small and large beaks. Individuals can disperse between habitats and mutate in their traits. We assume that local competition between individuals for common resources is a function of the distance in trait space between them (e.g. individual birds with similar-sized beaks compete more with each other than dissimilar ones as they utilize similar resources). Finally, we assume that the reproductive output of individuals is influenced by their abiotic environment and the match between the environment and their abiotic tolerance trait (u).

Given these general assumptions, the fitness of a focal individual in a given habitat is modelled as a function of its resource utilization trait (z ; e.g. beak size), abiotic tolerance trait (u ; e.g. physiological tolerance to temperature, influencing reproduction and survival), the z trait of all other individuals competing for the same resources locally, the local resource distribution, and local abiotic environmental conditions. These assumptions follow well-established precedents

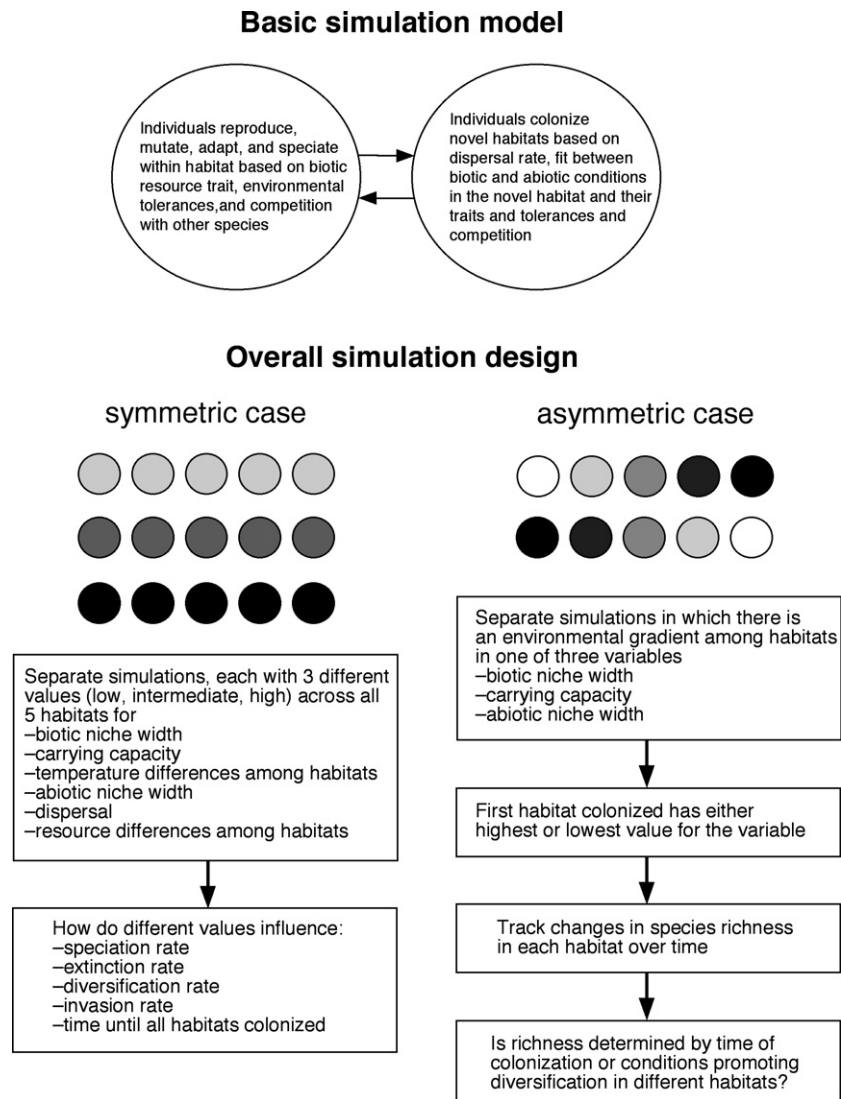


Figure 1 Diagrams illustrating the basic simulation model and the overall simulation design. The basic simulation model is to simulate the reproduction, mutation, adaptation and speciation of individuals within habitats over time (circles indicate each habitat). Individuals can also disperse between habitats (indicated with arrows between circles), based on their dispersal rate, their tolerance to abiotic conditions there, the fit of their biotic resource trait to local biotic resources and competition. Individuals that disperse may then speciate or remain as conspecific individuals distributed across multiple habitats. Speciation is determined by branching along trait axes (see Fig. 2). The overall simulation design involves a symmetric case (conditions identical across habitats, testing the impact of different variables on rates of speciation, extinction, diversification and colonization, and time until all habitats are colonized) and an asymmetric case (conditions differ across habitats, tracking richness in habitats over time).

in classic studies (e.g. Christiansen & Loeschcke, 1980; Brown & Vincent, 1987; Dieckmann & Doebeli, 1999).

We implement these assumptions in simulations that track the diversification of lineages in geographical space (habitats) and trait space. Below we specify the basic ecological model and describe our simulation algorithm. We then describe how speciation occurred, the species definition, the parameters examined, and our methods for evaluating the link between parameters, processes and richness patterns. Additional details of the model, model parameters, simulation methods and data analysis are provided in Appendix S1 in Supporting Information.

Ecological model

Under this model (and ignoring abiotic tolerances for now), the potential reproductive output (R) of a focal individual will be:

$$R(z, z, z_{\text{opt}}) = 1 + r \left(1 - \frac{\sum_j \alpha(z, z_j)}{K(z, z_{\text{opt}})} \right) \quad (1)$$

where

$$K(z, z_{\text{opt}}) = K_0 e^{-\frac{(z_{\text{opt}} - z)^2}{2\sigma_K^2}} \quad (2)$$

and

$$\alpha(z, z_j) = e^{-\frac{(z - z_j)^2}{2\sigma_\alpha^2}} \quad (3)$$

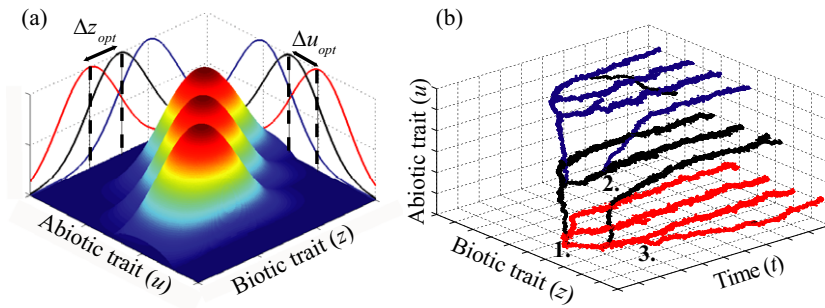


Figure 2 Illustrations of the model used. (a) An example of the fitness landscape in two-dimensional trait space as a function of resource distribution and abiotic conditions in three habitats (red, black, blue curves). Resource distribution and abiotic conditions are modelled as Gaussian functions of a biotic trait (z) and abiotic trait (u). Resource differences among habitats are denoted by Δz_{opt} and fitness in each habitat decreases as the resource trait z deviates from z_{opt} . Similarly, differences in abiotic conditions are denoted by Δu_{opt} with decreasing fitness as individuals deviate from u_{opt} . (b) An example of adaptive radiation in two-dimensional trait space among three habitats. Each individual's trait combination is plotted over time. Each line represents one species. Colour denotes different habitats. Speciation can occur through: colonization of novel habitats (denoted by 1 in b, individuals from habitat one (red) colonizes and radiates into habitat two (black)), colonization of an occupied habitat (denoted by 2, individuals from habitat two (black) colonizes and radiates into habitat three (blue)), and local speciation within a habitat (denoted by 3, speciation in habitat one (red)).

$K(z, z_{opt})$ represents the carrying capacity for a monomorphic population of individuals with trait value z in a habitat characterized by the point z_{opt} (Fig. 2). K_0 denotes the maximal carrying capacity (at $z = z_{opt}$), and the resource availability declines symmetrically as z deviates from z_{opt} according to the width of the resource distribution (σ_K). Note that this way of modelling carrying capacity is conceptually similar to a Lotka–Volterra population model. However, we utilize an individual-based approach and formulate reproductive output for a focal individual (i) as a function of the sum of its individual competitors (j), weighted by their interaction coefficient α_{ij} , and divided by carrying capacity. Equation 3 models the interaction coefficient, $\alpha(z, z_j)$, between the focal individual (defined by its trait z) and its competitors (defined by their traits z_j). Here, we standardize the competition coefficients so that, for a focal individual i , $\alpha_{ii} = 1$ and $0 < \alpha_{ij} < 1$ ($z_i \neq z_j$). σ_α determines the degree of competition between individuals given certain utilization traits and r denotes the intrinsic growth rate (equal for all individuals).

Including the abiotic variable as an effect on fitness, we define the realized reproductive output (fitness) of a focal individual as a fitness generating function (Dieckmann & Doebeli, 1999):

$$G(z, u, \mathbf{z}, z_{opt}, u_{opt}) = E(u, u_{opt}) * R(z, \mathbf{z}, z_{opt}) \quad (4)$$

where

$$E(u, u_{opt}) = e^{-\frac{(u_{opt}-u)^2}{2\sigma_u^2}} \quad (5)$$

$E(u, u_{opt})$ represents the effect of the abiotic environment as experienced by an individual with an abiotic trait value u in an environment characterized by u_{opt} (Fig. 2). Equation 5 equals one at $u = u_{opt}$ leading to the realized reproductive output (equation 4) being equal to the potential reproductive output (equation 1). However, realized reproduction

declines symmetrically as u deviates from u_{opt} according to σ_u and σ_u can thus be viewed as the abiotic environmental niche width.

Simulations

For each set of simulations (defined as a combination of biotic and abiotic conditions, specified below), we simulated alternating phases of reproduction and dispersal for 100,000 generations (time-step) and each simulation was replicated a total of 10 times (following Pontarp *et al.*, 2012, 2015). At the beginning of each simulation replicate, a habitat at the extreme end of the gradient was seeded with 10 monomorphic individuals. During reproduction, each individual reproduced according to its fitness and each offspring inherited the same trait values as their parent (asexual reproduction) unless the offspring mutated (see below). All offspring were born into the habitat of their parent, but dispersed with a probability (d) during the dispersal phase to one of the neighbouring habitats according to a stepping-stone dispersal algorithm (Pontarp *et al.*, 2012, 2015).

We followed all individuals, calculated their fitness, and allowed them to reproduce and disperse. As a result, the simulation output is a distribution of individuals in trait space and geographical space for each time-step (Fig. 2). The mutation process (with offspring values close to parental values), together with the evolutionary process (driven by the fitness generating function), generates a clustered distribution of trait values along the trait axes (Fig. 2). We treat these clusters of similar individuals as species (Pontarp *et al.*, 2012, 2015). See Appendix S1 for details.

Results were very similar among replicates, strongly suggesting that 10 replicates were adequate. In our main analysis, we assumed that speciation is driven by local adaptation

and disruptive selection (e.g. ecological speciation; Schluter, 2009; Nosil, 2012). We also performed a set of simulations incorporating non-ecological speciation, which gave similar results (see Appendix S2 in Supporting Information).

Speciation

Speciation occurred both within and between habitats (see Appendix S1 for detailed description). At the local scale (within habitats), clusters of individuals (species) with similar phenotype branched into distinct clusters in trait space (Fig. 2), representing speciation (e.g. Geritz *et al.*, 1998; Dieckmann & Doebeli, 1999; Pontarp *et al.*, 2012, 2015). The diversification process continued until new species were prone to stochastic extinctions due to decreased population sizes and weak disruptive selection (e.g. Johansson & Ripa, 2006; Claessen *et al.*, 2007; Johansson *et al.*, 2010).

Speciation also occurred between habitats. Given that individuals disperse between habitats, individuals from a particular species could establish in several habitats if they had positive fitness after colonization of each habitat. Differences between habitats in abiotic conditions (Δu_{opt} ; temperature hereafter) and/or resource types (Δz_{opt}) could then lead to disruptive selection and allopatric speciation. Here, dispersal is defined as the probability that each offspring disperses from the parental habitat to a neighbouring habitat. Note that dispersal is a parameter of the model, whereas establishment of dispersing individuals is part of our results (see below).

Species were defined as groups of individuals having common descent and a continuous distribution of traits (no gaps in the trait distribution > 0.1) in both trait dimensions (resource utilization, abiotic tolerance). This definition was independent of which habitat individuals occurred in, such that a single species could occur in multiple habitats. When a gap > 0.1 was detected in either trait dimension within an existing species, it was considered a speciation event (i.e. one species branching into two). These clusters of similar individuals (species) appeared to be distinct and stable over time.

The specific value of 0.1 was chosen following Pontarp *et al.* (2015). Smaller thresholds would lead to more speciation events but with species that were non-viable. A larger limit would lead to discrepancies between registered speciation events and the clusters that were obvious from visual inspection of the simulation outputs. A limit of 0.1 also makes biological sense in the context of our simulations as it is large enough to prevent speciation by only a few mutations. Furthermore, the smallest niche width we used in our simulations was also 0.1. Thus, we required a separation of at least one niche width to count a cluster as a species.

Simulation design and data analysis

Based on preliminary simulations that extensively varied many parameters, we identified several key parameters that

most strongly influenced richness patterns among habitats. These parameters were: abiotic differences between habitats (Δu_{opt}), biotic resource differences between habitats (Δz_{opt}), biotic niche widths (σ_x), abiotic niche widths (σ_u), carrying capacity (K_0) and dispersal probability (d). See Table 1 for default values and Appendix S1 for justification of the parameter space examined.

We first explored the impact of different parameter values on richness patterns and the underlying processes (specific values in Table 1). Although the specific values examined are somewhat arbitrary, they nevertheless provide insights on how changing the values influences the direction of changes in richness (Fig. 3) and the mechanisms by which these changes occur (Fig. 4). More specifically, to understand how ecological variables influenced the processes that directly influenced richness, we estimated the time (in generations) until all habitats were colonized and also the rates of speciation, extinction and colonization of habitats (as events per unit time, over the time course of the simulation). We then analysed richness patterns when all five habitats had the same conditions for high, intermediate, and large values of each parameter separately (Table 1). We refer to this as the symmetric case.

We also analysed cases in which three key variables differed among habitats (mean biotic niche width, abiotic niche width and carrying capacity) and tracked the species richness in habitats over time (Fig. 5). We refer to this as the asymmetric case. Each of these three variables varied across habitats, and all other parameters were held constant (see Table 1). For each variable, a set of simulations was run with the variable forming a gradient in a different direction among habitats (e.g. the seeded habitat, habitat 1, had the lowest carrying capacity versus the highest carrying capacity). These analyses were used to compare the relative impact of time and diversification rates on richness patterns among habitats. Specifically, under the time hypothesis, the seeded habitat should have the highest richness (regardless of variable values), whereas under the diversification-rate hypothesis, the habitat with variable values that increased diversification should have the highest richness (regardless of which was the seeded habitat).

We tested whether net diversification rates (rates of speciation-extinction) were correlated with the final, local species richness of each habitat in the asymmetric case, and with values of the three variables that varied among habitats (biotic niche width, abiotic niche width, and carrying capacity). Rates for each habitat were estimated as the number of events (speciation, extinction, diversification [speciation - extinction]) divided by the time of colonization of that habitat. A separate correlation analysis was conducted in each of the six asymmetric cases examined here, with habitats as the units of analyses (based on mean values for each habitat from all 10 replicates).

We also examined patterns of speciation and extinction in these habitats over time in the asymmetric case (Fig. S5 in Appendix S3). However, given space limitations, we do not discuss these results in detail.

Table 1 Parameter values used in the simulations, with values either the same (symmetric) or different (asymmetric) across habitats. First, richness patterns were analysed for small, intermediate and large values (evenly distributed throughout parameter space) for seven of the model parameters separately. Local conditions were identical among habitats (symmetric case) and defined by default parameter values (underlined). Second, patterns were analysed in simulations when biotic and abiotic niche width and carrying capacity differed (asymmetric case) among habitats. See specific units and explanation for these variables in Methods and Appendix S1.

Symmetric					
Parameters	Small	Intermediate	Large		
Abiotic differences between habitats (Δu_{opt})	0.1	<u>0.5</u>	1.0		
Resource differences between habitats (Δz_{opt})	0.1	<u>0.5</u>	1.0		
Biotic niche widths (σ_a)	0.1	<u>0.2</u>	0.3		
Abiotic niche widths (σ_u)	0.5	<u>1.0</u>	1.75		
Carrying capacity (K_0)	500	<u>1500</u>	2500		
Dispersal probability (d)	0.001	<u>0.01</u>	0.1		
Resource distribution width (σ_K)	1.0	<u>1.0</u>	1.0		
Asymmetric					
Parameters	Habitat				
	1	2	3	4	5
Abiotic differences between habitats (Δu_{opt})	0.5	0.5	0.5	0.5	0.5
Resource differences between habitats (Δz_{opt})	0.5	0.5	0.5	0.5	0.5
Biotic niche widths (σ_a)	0.1	0.2	0.3	0.4	0.5
Abiotic niche widths (σ_u)	1.5	1.25	1.0	0.75	0.5
Carrying capacity (K_0)	500	1000	1500	2000	2500
Dispersal probability (d)	0.01	0.01	0.01	0.01	0.01
Resource distribution width (σ_K)	1.0	1.0	1.0	1.0	1.0

Sample simulation results (richness in each habitat over time) are illustrated in Figs S1–S3 in Appendix S3. These are each based on a single replicate (for ease of visualization), but results are similar when including all 10 replicates (Figs 3–5).

RESULTS

We first analysed how different parameters influenced overall richness (total number of species across all habitats), with parameter values equal across the five habitats (Table 1). Additional theoretical background and discussion of mechanisms is provided in Appendix S1.

Biotic niche width (σ_a) strongly influenced overall richness patterns, with narrower niche specialization driving higher richness (Fig. 3). High local carrying capacity (K_0) also promoted higher overall species richness (Fig. 3b). Small temperature differences between habitats (Δu_{opt}), wide abiotic niche width (σ_u) and high dispersal probability (d) all reduced richness (Fig. 3c,e), presumably by facilitating movement between

habitats and thereby disrupting speciation (e.g. Brown & Pavlovic, 1992; Mizera & Meszina, 2003; Parvinen & Egas, 2004). Variation in resource differences among habitats (Δz_{opt}) had little effect on richness (Fig. 3f), although smaller resource differences led to slightly higher richness.

Additional analyses (Fig. 4) revealed how these parameters were related to the processes that directly control species richness (speciation, extinction, dispersal; see also Appendix S1). The biotic (resource) niche width (σ_a) influenced both speciation and extinction rates (events per generation), with narrower niche widths increasing both speciation and extinction (Fig. 4a,b). Low carrying capacity decreased both speciation and extinction rates. Other variables had less impact on speciation and extinction rates. Diversification rates (speciation - extinction rates) were higher with narrow biotic niche widths and lower with low carrying capacity and small temperature differences among habitats (Fig. 4e). The number of generations until all habitats were colonized (when a species established a population size of ten or more individuals in a habitat in which no other species were established) was strongly and positively related to differences in temperature among habitats (Δu_{opt}), with small differences between habitats decreasing the time until all habitats were colonized (Fig. 4c). Resource differences among habitats also had a positive relationship with colonization time (albeit a weaker one). Carrying capacity, abiotic niche width, and dispersal probability all showed negative relationships with colonization time (Fig. 4c). We found a strong positive relationship between invasion (when a species invaded an already colonized habitat) rate and abiotic niche width (Fig. 4d). Most other parameters were weakly and negatively related to invasion rate (e.g. biotic niche width, carrying capacity). Surprisingly, low dispersal probability (set by parameter d) was strongly related to high rates of invasion.

Most importantly, we examined patterns of species richness in the five habitats over time when ecological parameters varied across habitats (Fig. 5). Note that habitat 1 (seeded habitat) was always colonized first. Biotic niche width had a dramatic impact on patterns of richness in habitats over time (Fig. 5a,b), seemingly through the impacts of niche width on speciation, with narrower niches increasing speciation and diversification rates (Fig. 4). Nevertheless, these results showed that the time-for-speciation effect determined patterns of species richness over short time-scales, even under conditions where variation in diversification rates eventually dominated richness patterns. Specifically, when biotic niche widths were wider in habitat 1 (conditions that reduce speciation), habitat 1 and the adjacent habitat 2 initially had the highest richness. Habitat 5 was not colonized until ~40,000 generations. However, after that point, habitats 4 and 5 quickly increased in richness until they had the highest richness. In other words, the richness gradient ‘flipped’ over the course of the simulation, showing a strong time-for-speciation effect initially but the impact of diversification rates later.

In contrast, when biotic niche widths were narrower in habitat 1, then habitats 1 and 2 quickly developed and

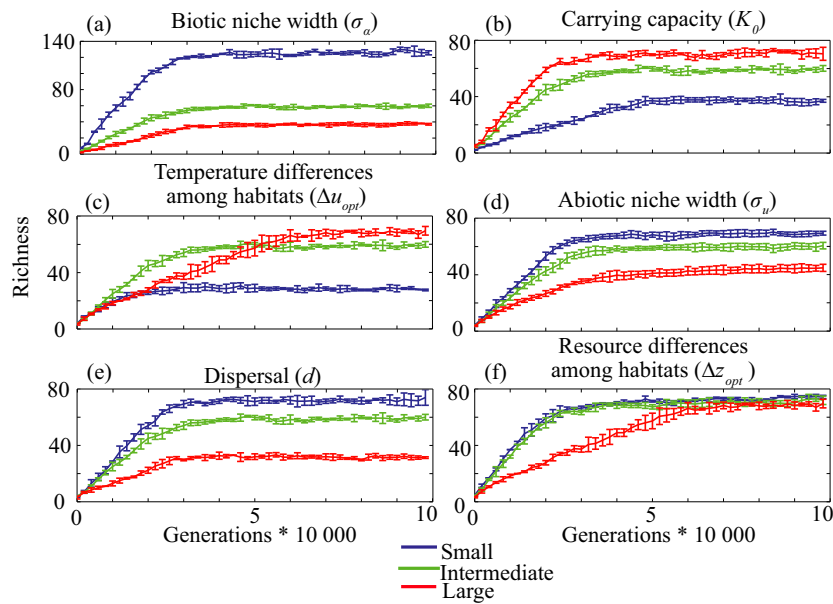


Figure 3 Accumulation of regional richness over time (total number of unique species, summed across all habitats) calculated as the mean (lines) and standard deviation (error bars) of 10 replicated simulations. Note the substantially higher richness values in (a): all other y -axes are identical. Simulations were run for small, large, and intermediate values of six model parameters (see title of each panel): note that these different values are evenly distributed within a variable but are not necessarily equivalent between variables (see Table 1). All other parameters were set to default values (Table 1). Local conditions such as niche widths and resource amounts were equal among habitats.

maintained the highest richness throughout the simulation. Interestingly, richness increased slowly over time in habitats 3, 4 and 5. Habitat 5 was not colonized until 30,000 generations had been reached. Overall, we found the consistently strongest species richness gradient (greatest differences between the most species-rich and species-poor habitats over time) under these conditions, when the time-for-speciation effect and environmental impacts on diversification favoured higher species richness in the same habitats.

The results in which carrying capacity varied among habitats showed strong parallels to those for biotic niche width (Fig. 5c,d). First, when carrying capacity was lowest in habitat 1, the gradient in richness again ‘flipped’ over the course of the simulation, with higher richness in habitats 1 and 2 until $\sim 30,000$ generations were reached, and higher richness in habitats 3, 4 and 5 after 50,000 (although habitat 5 never had the highest richness). Second, when the carrying capacity was highest in habitat 1, this habitat had relatively high richness throughout the simulation. Third, regardless of whether the carrying capacity was low or high in habitat 5, this habitat was not colonized until after 30,000 generations.

This latter pattern (late colonization of habitat 5) may seem surprising given that habitat 5 has many resources (high carrying capacity) and no species occupying it. However, these results show that colonization of a new habitat requires many individuals (or species) in the adjacent habitat (i.e. more potential dispersers). For example, regardless of whether carrying capacities were high or low in habitats 4

and 5, habitat 4 was only colonized when there were ~ 10 species in habitat 3, and habitat 5 was only colonized when there were ~ 10 species in habitat 4 (Fig. 5). Thus, carrying capacity impacted the colonization of habitats through the number of dispersers available in adjacent habitats.

Variation in abiotic niche width across habitats generally had little effect on richness patterns over time (Fig. 5e,f). Nevertheless, there was a greater time-for-speciation effect as niche width decreased from habitat 1 to 5 (Fig. 5f), such that more time was required to colonize habitats with narrower niche widths (as in Fig. 3c).

To test the robustness of the results on richness in habitats over time (Fig. 5), we repeated these analyses after incorporating non-ecological speciation. Richness patterns were very similar (Table S1 and Fig. S4 in Appendix S3). Most importantly, our conclusions were upheld about the initial importance of the time-for-speciation effect and later importance of diversification rates.

We also examined the relationships between net diversification rates, values for the three ecological variables among habitats (abiotic and biotic niche widths, carrying capacity), and the final local richness of each habitat. Correlation coefficients (r) and P -values (P) presented below are associated with our two asymmetric cases (hence two r and P -values for each relationship presented) with decreasing and increasing ecological variables across habitats (see also Table S2 in Appendix S3). Net diversification rates were strongly related to local richness when carrying capacity varied among habitats ($r = 0.94, 0.89$; $P = 0.02, 0.04$), and the relationship between carrying capacity

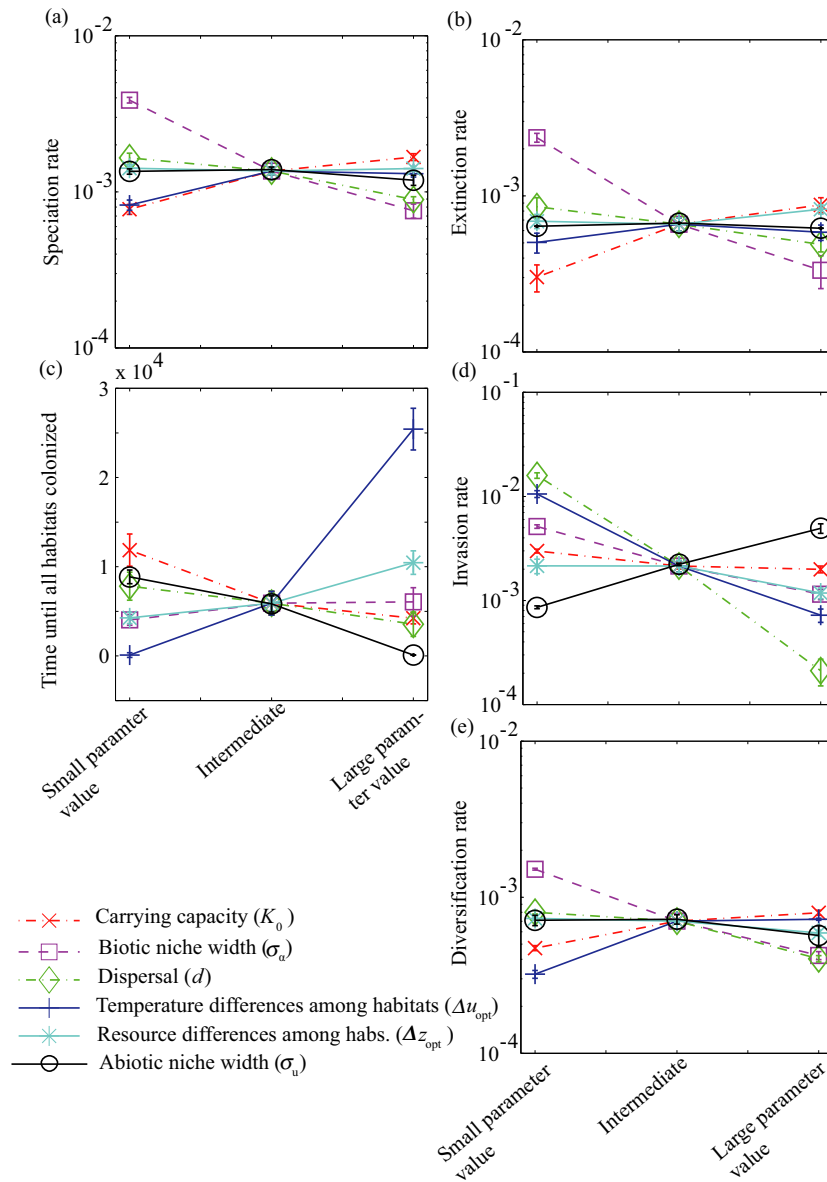


Figure 4 The impact of six model parameters on relevant processes, including speciation rate (a), extinction rate (b), time until all habitats were colonized (c), invasion rate (d) and diversification rate (e) that drive richness patterns among habitats. Note that small, medium and large values are evenly distributed within a variable but are not necessarily equivalent between variables (see Table 1). All other parameters were set to default values (Table 1). Local conditions such as niche widths and resource amounts were equal among habitats. The results show the mean (point symbols) and standard deviation (error bars) for 10 replicated simulations.

and diversification rate ($r = 0.68, 0.91; P = 0.21, 0.03$) could be stronger than the relationship between carrying capacity and local richness ($r = 0.73, 0.70; P = 0.16, 0.19$). When biotic niche width varied among habitats, biotic niche width was strongly related to both local richness ($r = 0.93, 0.91; P = 0.02, 0.03$) and diversification rate ($r = 0.89, 0.92; P = 0.04, 0.03$). The relationship between diversification rate and local richness under these conditions was similar, but only marginally significant ($rc = 0.84, 0.85; P = 0.08, 0.07$). Relationships between abiotic niche width, net diversification, and local richness were weak and non-significant (Table S2 in Appendix S3). Overall, these results demonstrate that finite

carrying capacities do not make net diversification rates meaningless or misleading (contra Rabosky, 2009). Instead, more limited carrying capacities in some habitats can influence overall richness patterns among habitats through their impacts on net diversification rates in each habitat.

DISCUSSION

Overview

Relatively few studies have used simulations to elucidate the interplay of evolutionary and ecological processes that drive

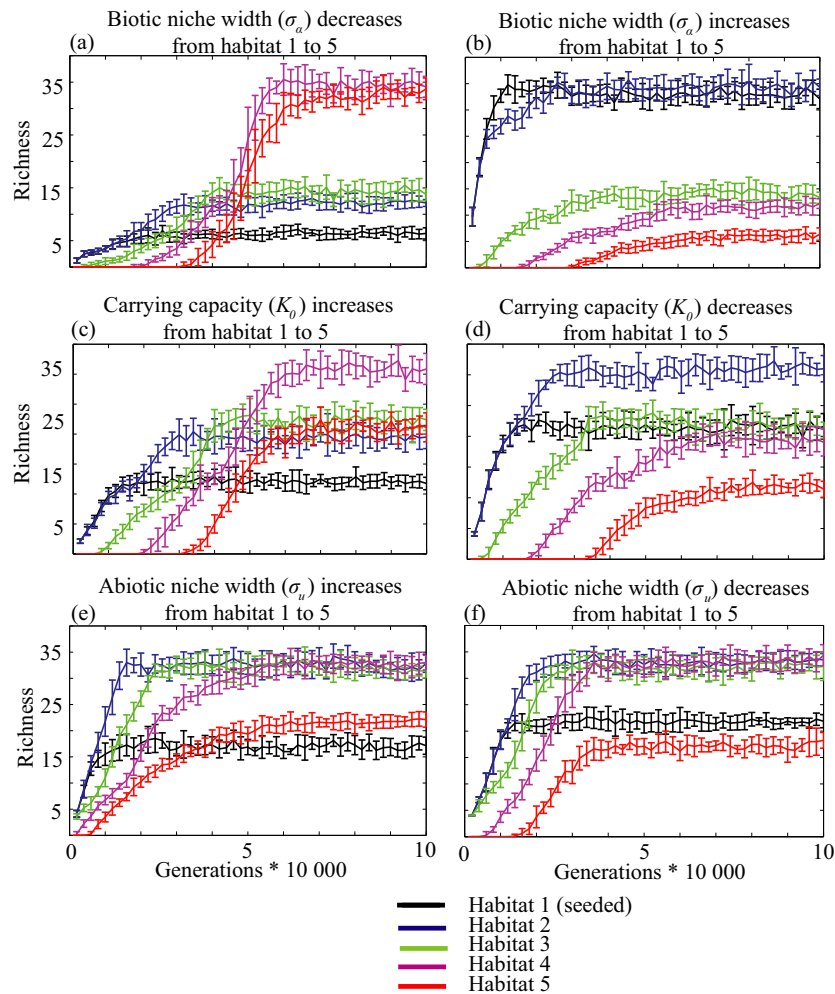


Figure 5 Accumulation of local richness over time in each of the five habitats calculated as the mean (lines) and standard deviation (error bars) of 10 replicated simulations. Local ecological conditions (see title of each panel) differed among habitats along the environmental gradient. All other parameters were set to default values (Table 1).

species richness patterns among habitats, especially the relative importance of time, diversification rates and carrying capacity. Our study offers three general insights.

First, our results provide an explanation for why some empirical studies support the time-for-speciation effect as a cause of richness patterns, whereas others support diversification rates instead. We find that the time-for-speciation effect can have a strong influence on patterns of species richness among habitats over shorter time-scales. This is most apparent in our simulations (Fig. 5) in which the clade originates in habitats that have wide biotic niche widths or low carrying capacities (conditions which lower rates of diversification). There is initially higher species richness in habitats colonized first (relative to habitats colonized later), but when all habitats are colonized the habitats with conditions that promote diversification ‘catch up’ and eventually have the highest richness. Thus, we show that diversification rates and the time-for-speciation effect could explain contrasting richness patterns along the same ecological gradient, but at different points of time.

This set of results provides theoretical support for the idea that the time-for-speciation effect may be most important for explaining richness patterns over shorter spatial and temporal scales (e.g. within regions, in smaller clades), and diversification rates over larger spatial and temporal scales (e.g. the latitudinal diversity gradient; Rabosky, 2009; Wiens, 2011). Our results may also help explain why studies of younger clades often fail to find a latitudinal gradient in diversification rates, whereas analyses of older clades often do (e.g. studies within frog families versus across amphibians: Wiens *et al.*, 2006, 2009 versus Pyron & Wiens, 2013; studies within mammal genera versus across mammals: Soria-Carrasco & Castresana, 2012 versus Rolland *et al.*, 2014). These results might also help explain the reverse latitudinal richness gradient in some young subclades (i.e. higher temperate diversity) within older groups that show high tropical richness overall (e.g. mammals: Buckley *et al.*, 2010). Some of these results also have precedents in the simulation results of Hurlbert & Stegen (2014) who showed an inverse latitudinal gradient arising before equilibrium richness

was reached, although a latitudinal gradient arose eventually after equilibrium (their Fig. 2b), given a temperate origin and strong ecological limits.

Second, our results call into question the idea that carrying capacity, time, and diversification rates represent three competing explanations for richness patterns (as in fig. 1 of Mittelbach *et al.*, 2007). Our results suggest that carrying capacity should instead be viewed as an ecological factor that can influence both diversification rates and time, rather than a direct explanation for richness patterns (just as climate is not itself a direct explanation for richness patterns). We found that low carrying capacities and wide resource niche widths lead to reduced rates of speciation and diversification (Fig. 4) and lower overall richness (Fig. 3). Hence, carrying capacities and ecological limits are not alternative paradigms relative to diversification rates. Instead, they are important ecological factors that can potentially influence net speciation and extinction over time (along with many other factors).

Similarly, we found that explanations for richness patterns based on the time-for-speciation effect and carrying capacity of habitats can also be linked rather than competing. We found that limited carrying capacities in some habitats may increase the time until they are colonized (Fig. 4) and thereby underlie the time-for-speciation effect. We also found strong richness gradients caused by differences in the timing of colonization when carrying capacity varied across habitats (Fig. 5), regardless of whether the seeded habitat had high or low carrying capacity. These results also suggest how factors related to species interactions (e.g. limited carrying capacity, wide biotic niche widths) could influence dispersal between habitats over time and act as an underlying cause of niche conservatism (i.e. Wiens *et al.*, 2010).

In summary, these latter results suggest that carrying capacity, time-for-speciation and diversification rates are not competing explanations or alternative paradigms. Instead, we found that carrying capacity is an important ecological factor that can influence both diversification rates (by impacting speciation and extinction) and time-for-speciation (by impacting when habitats are colonized). But carrying capacity itself is not a direct explanation for richness patterns, and like other ecological factors (e.g. climate), it can only impact richness by influencing rates and patterns of speciation, extinction and dispersal.

Third, our results raise the possibility that biotic (resource-based) niche width may be more important for driving species-richness patterns than carrying capacity itself (Figs 2 & 3). For example, simply increasing a limiting resource may increase the number of individuals of a given species in a given habitat, but need not increase the number of species. Instead, it is a narrow biotic niche width that may be particularly important for allowing species to partition resources, diverge, speciate and co-exist.

Assumptions and limitations

In this study, we used a generalized, individual-based model that minimized *a priori* assumptions about the evolutionary

and ecological processes that generate species richness patterns. However, as in any simulation study, we still made several assumptions that may or may not impact our conclusions. First, our main results (Figs 3–5) are based on simulated speciation that occurs through ecological divergence. There is growing evidence that ecological divergence is important in speciation (reviews in Schluter, 2009; Nosil, 2012), but there is also evidence that ecological similarity over time (niche conservatism) can drive allopatric speciation initially (e.g. Kozak & Wiens, 2006; Hua & Wiens, 2013). However, we also show that our main conclusions are robust to including non-ecological speciation (see Fig. S4 in Appendix S3).

We assume that environments have finite carrying capacities that limit their richness over long time-scales. It is unclear if this is generally a realistic model (e.g. Wiens, 2011; Harmon & Harrison, 2014). For example, species can potentially evolve to utilize new resources, thus launching clades into new 'adaptive zones' and driving new radiations with minimal competition with existing radiations (e.g. Schluter, 2000). Regardless, patterns that occur before these limits are reached can be readily observed in our simulations (Fig. 5). Furthermore, a major goal of our study was to evaluate the implications of finite carrying capacity for the origin of richness patterns.

A major assumption of our study is that we model asexual organisms. However, it seems that our major results should be robust to this assumption. We think that the only practical implication of this assumption is that we do not explicitly model speciation as the evolution of intrinsic reproductive isolating mechanisms (e.g. Coyne & Orr, 2004). Instead, we assume that speciation occurs largely through ecological divergence (a process widely known to be important in speciation in sexual organisms; Schluter, 2009; Nosil, 2012). It would be interesting to model the evolution of isolating mechanisms in sexual organisms and relevant approaches already exist (e.g. Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2003; Heinz *et al.*, 2009; Gilman & Behm, 2011). However, this would be difficult to apply to our simulations of hundreds of species, due to the computational cost of the increased model complexity. Most importantly, it is unclear if this would impact our results at all, given the demonstrated robustness of our main results to incorporating non-ecological speciation (Fig. S4 in Appendix S3).

Furthermore, the linear arrangement of habitats we assumed here may not apply universally, and in some cases influenced our results. For example, we sometimes observed the highest richness in habitats 2 or 4, even when conditions favouring speciation were higher in habitats 1 or 5 (Fig. 5). This occurred because 'middle' habitats can share species with habitats on either side, whereas 'end' habitats only share species with one adjacent habitat. Nevertheless, this linear arrangement of habitats may apply to many empirical systems such as elevational and latitudinal gradients.

Finally, we note that there are several other assumptions in our simulations (e.g. non-overlapping generations,

temporally stable environments). For many of these assumptions, we can see no plausible mechanism by which they would overturn our conclusions about the origin of richness patterns. For others, violating these assumptions might influence our results (e.g. mass extinction events in some habitats). However, trying to include every potentially realistic detail is not practical and would detract from our goal of understanding how the focal processes of our study generate richness patterns. Moreover, our results are broadly consistent with many empirical studies and should thus provide insights into the general processes that underlie diversity patterns, even if they do not perfectly mimic the details of any particular empirical system.

CONCLUSIONS

We explore the origins of richness patterns along environmental gradients, and the widespread paradigm that time, diversification rates and carrying capacities are competing explanations for species richness patterns. We find that these explanations can be intertwined rather than competing. Specifically, we find that carrying capacity can influence both diversification rates and the time-for-speciation effect but may not itself be a direct explanation for richness patterns (like climate).

We also illuminate why some richness gradients are explained by diversification rates and others by time. We show that 'young' gradients (i.e. in young clades or subclades) seem most likely to be explained by time and 'old' gradients by differences in diversification rates across the gradient. Thus, our results may help reconcile the seemingly conflicting results of many empirical studies of the evolutionary and ecological origins of richness gradients.

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of Amazonian megadiversity. *Ecology Letters*, **14**, 643–652.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Parameters, biotic/abiotic conditions, eco-evolutionary processes.

Appendix S2. Non-ecological speciation and mutation rate.

Appendix S3. Supplementary tables and figures.

BIOSKETCHES

Mikael Pontarp is a postdoctoral fellow at the Institute of Evolutionary Biology and Environmental Studies at the University of Zurich. He studies the link between fundamental ecological, evolutionary and biogeographical assembly processes and community patterns such as diversity, trait distribution and phylogenetic structure. To this end, Mikael uses a wide variety of eco-evolutionary modelling and simulation approaches.

John J. Wiens is a professor in the Department of Ecology and Evolutionary Biology at the University of Arizona. His main interest is in using integrative phylogenetic approaches to address conceptual questions at the interface of ecology and evolutionary biology, including species richness, speciation, niche evolution and species responses to climate change.

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