IDEA AND PERSPECTIVE

The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity

Héctor T. Arita* and Ella Vázquez-Domínguez

Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, CP 04510, México DF, Mexico

Correspondence: E-mail: arita@ecologia.unam.mx

Abstract

Several ecological and evolutionary hypotheses have been proposed to explain the latitudinal diversity gradient (LDG), but a general model for this conspicuous pattern remains elusive. Mid-domain effect (MDE) models generate gradients of species diversity by randomly placing the geographic ranges of species in one- or two-dimensional spaces, thus excluding both evolutionary processes and the effect of contemporary climate. Traditional MDE models are statistical and static because they determine the size of ranges either randomly or based on empirical frequency distributions. Here we present a simple dynamic null model for the LDG that simulates stochastic processes of range shifts, extinction and speciation. The model predicts higher species diversity and higher extinction and speciation rates in the tropics, and a strong influence of range movements in shaping the LDG. These null expectations should be taken into consideration in studies aimed at understanding the many factors that generate latitudinal diversity gradients.

Keywords

Distribution, diversity, extinction, geographic range, latitudinal gradient, mid-domain effect, null models, speciation, stochastic processes.

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INTRODUCTION

The latitudinal diversity gradient, in which species richness decreases away from the tropics, is the most conspicuous pattern in biogeography (Rosenzweig 1995; Willig *et al.* 2003). This general pattern has been documented for marine and terrestrial systems, for several groups of animals, plants and microorganisms, and has persisted, with some variations, through geological time (Crame 2001; Hillebrand 2004). Despite its ubiquity, a general explanation for the gradient remains elusive, and over 30 ecological and evolutionary processes have been proposed to account for such a striking pattern (Willig *et al.* 2003; Mittelbach *et al.* 2007).

Traditional ecological explanations have focussed on local, deterministic mechanisms allowing the coexistence of more interacting species in tropical localities than in temperate areas through processes such as species packing and niche partitioning. More recently, ecologists have developed accurate models of large-scale diversity as a function of area, climate and energy availability (Hawkins *et al.* 2003; Kalmar & Currie 2007). Similarly, climate in the past has also been shown to be a determining factor in explaining the geological history of latitudinal patterns of diversity (Powell 2007). The underlying idea of many of these studies is that more productive environments can sustain more individuals and therefore can support more species. However, alternative explanations have been put forward, including the hypothesis that higher levels of energy might promote higher rates of speciation, either through more intense species interactions or through faster evolutionary rates (Currie *et al.* 2004; Allen & Gillooly 2006; Allen *et al.* 2006; but see Bromham & Cardillo 2003). This view recognizes the importance of evolutionary and historical factors in shaping present-day ecological patterns (Ricklefs 2007).

Evolutionary hypotheses for the latitudinal gradient of diversity have focussed on how different rates of origination and extinction in tropical and extratropical areas might determine the equilibrium number of species (Mittelbach

et al. 2007). According to the area hypothesis, for example, the larger surface available in tropical areas fosters higher speciation rates, because of increased probabilities of geographic isolation, and lower extinction rates, due to larger population sizes (Rosenzweig 1995). Alternatively, if diversification rate is equal in tropical and extratropical regions, the tropics could still be more diverse if tropical environments are older and have had more time to generate species (the time hypothesis). Besides speciation and extinction, shifts in the geographic ranges of species might affect the structure of the latitudinal gradient of diversity (Martin *et al.* 2007). According to the niche-conservatism hypothesis, for example, dispersal of tropical groups to temperate areas is limited by environmental conditions, leaving less time for speciation outside the tropics (Wiens & Donoghue 2004; Wiens *et al.* 2006).

Evolutionary hypotheses can be summarized in three general models that derive from Stebbins' concept of tropical cradles and museums (Stebbins 1974; Chown & Gaston 2000; Jablonski *et al.* 2006; Fig. 1). In the 'tropics as cradle' model, origination rate is higher in the tropics and extinction rate is constant (Fig. 1a). In the 'tropics as museum' hypothesis, origination rate is constant and extinction rate is lower in the tropics (Fig. 1b). In the 'out of the tropics' postulate, tropical areas have both a higher origination rate and a lower extinction rate, and there is a positive net movement of species from the tropics to extratropical areas (Jablonski *et al.* 2006; Fig. 1c). In the three cases, net diversification rate (origination minus extinction rates) is higher in the tropics, explaining the latitudinal diversity gradient. These are extreme cases that are not mutually exclusive, and most real systems are likely to show different combinations of the three (Stenseth 1984; Wiens & Donoghue 2004; McKenna & Farrell 2006).

A major obstacle in testing evolutionary hypotheses on the origin of the latitudinal gradient of species is the impossibility of measuring directly the rates of origination, extinction and dispersal through evolutionary time. Researchers have relied on inferences made from the fossil record or from present-day patterns of biogeography (Buzas *et al.* 2002; Allen & Gilooly 2006; Jablonski *et al.* 2006; Martin *et al.* 2007; Weir & Schluter 2007). A complementary approach is to develop models that simulate the dynamics of speciation, extinction and dispersal to test evolutionary hypotheses (Goldberg *et al.* 2005; Roy & Goldberg 2007).

Here we present a model specifically designed to test hypotheses on the mechanisms that could generate latitudinal gradients of species diversity. It is based on a very simple simulation of shifts in the geographic distribution of species that makes very few assumptions. Although dynamic and stochastic in nature, our model is not intended to be predictive or explanatory, as neutral models for ecological
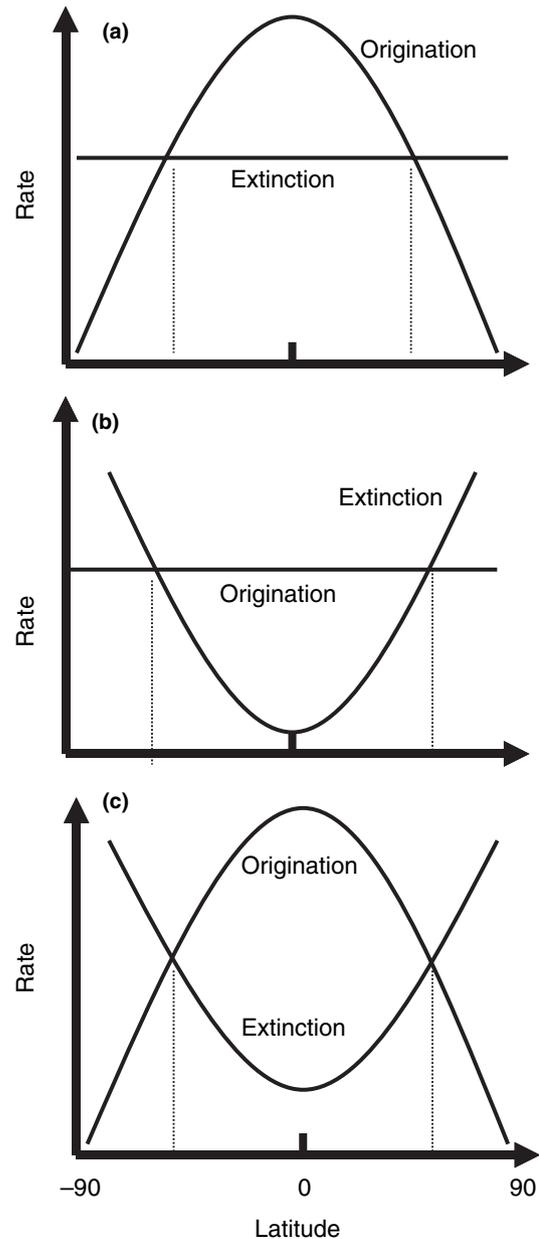

Figure 1 Three possible patterns of diversification to explain the higher diversity of tropical areas. (a) In the 'tropics as cradle' model, origination rate is higher in tropical areas and extinction rate is equal in both zones. (b) In the 'tropics as museum' model, origination rate is the same for tropical and extratropical areas, but extinction rate is lower in the tropics. (c) In the 'out of the tropics' model, origination rate is higher, extinction rate is equal or lower in tropical areas, and species movement is higher from the tropics to the extratropical areas. In all cases, the diversification rate (origination minus extinction) is higher in tropical areas.

communities are. Rather, we conceive our simulations as null models for testing hypotheses on the latitudinal gradient of species diversity (Gotelli & McGill 2006).

DYNAMIC MODEL

Dynamics of species ranges

We modelled a latitudinal gradient with a one-dimensional domain, arbitrarily setting the lower ('south') boundary to 0.0 and the upper ('north') boundary to 1.0 (Colwell & Lees 2000). We defined three equal-sized bands along the domain: (i) the 'southern extratropical' band, extending from 0.0 to 0.33; (ii) the 'tropical' band, from 0.33 to 0.67; and (iii) the 'northern extratropical' band, spanning from 0.67 to 1.0. The geographic range of a species was defined by the position of its southern (L_1) and northern (L_2) limits, which were points that could take any value along the domain ($0.0 \leq L_1$, $L_2 \leq 1.0$, $L_1 \leq L_2$). Range size, measured as a latitudinal extent, was defined as $R = L_2 - L_1$, and range midpoint as $M = (L_2 + L_1)/2$.

To simulate shifts in the range of a species, we left L_1 and L_2 to follow random-walk processes. In each time step, each limit varied its position by a random distance sampled from a uniform distribution $U(-D, D)$. Thus, the movements of L_1 and L_2 were independent of each other, simulating stochastic responses to environmental conditions in different parts of the domain (Fig. 2a). The restriction $0.0 \leq L_1$, $L_2 \leq 1.0$ was enforced with 'absorbing' boundaries that refrained L_2 and L_1 to wander beyond the domain but that allowed them to be 'reflected' in subsequent steps. In preliminary runs of the model, we created sets of 10 000 species and allowed the ranges to shift stochastically for 4000 time steps with $D = 0.01$. We tested different initial conditions, including the extreme cases where all species occupied the whole domain ($L_1 = 0.0$, $L_2 = 1.0$ for all species) to cases where species were limited to a single random point along the domain: $L_1 = L_2 = L$, where L was a random number in the interval (0.0, 1.0). Species richness at a given point along the domain was computed as the number of ranges intersecting that point.

In all these preliminary runs, regardless of the initial conditions, the end results were indistinguishable from those of the fully stochastic version of the mid-domain model, in which the position of L_1 and L_2 is set by sampling from a uniform distribution $U(0.0, 1.0)$: (i) a parabolic function of species richness (S) with domain position x ($S = 2x - 2x^2$), with a peak in species richness at the centre of the domain ($x = 0.5$); (ii) points in a scatter plot of range size vs. midpoint position arranged within a triangle defined by the geometric constraints of a bounded domain; (iii) a range-size frequency distribution following a linear decreasing function with mean 0.33 and variance 0.055 and (iv) no gradient of average range size along the domain (Colwell & Hurtt 1994; Willig & Lyons 1998; Colwell & Lees 2000; Arita 2005).
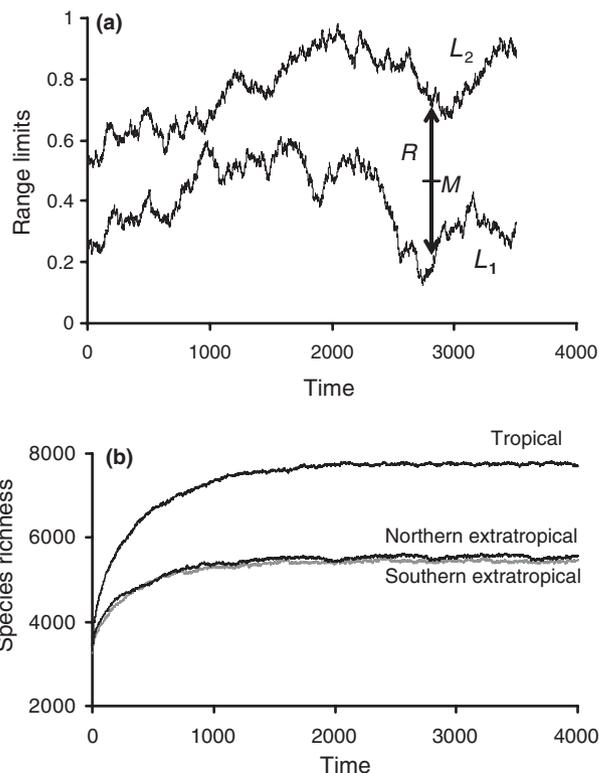

Figure 2 Random-walk simulation of the dynamics of distributional ranges. (a) The range size (R) and midpoint position of the range (M) of a given species are determined by the stochastic movements of the lower (L_1) and upper (L_2) limits of the range along a latitudinal gradient. (b) Dynamics of species richness resulting from stochastic shifts in the range of 1000 species in three latitudinal bands: southern extratropical species occur from 0.0 to 0.33 along the domain, tropical species occur between 0.33 and 0.67 and northern extratropical species occur between 0.67 and 1.0.

Species richness in the three latitudinal bands also conformed to expectations of mid-domain models. Figure 2b shows the results of a simulation that started with 10 000 species, each confined to a single random point along the domain. Initial species richness was equal for the three bands (3435 for the tropical band, and 3255 and 3310 for the extratropical bands, or *c.* 33% of all species in each band). After a few thousand steps of random-walk range shifts, diversity stabilized at *c.* 5555 species for each of the extratropical bands and 7777 species for the tropical band. The expected proportional richness is 5/9 (0.555) and 7/9 (0.777), respectively, using the formula $S = 2x_2 - x_2^2 - x_1^2$, where x_1 and x_2 are the lower and upper limits of a region along the domain, respectively (Arita *et al.* 2005). In additional simulations with different initial conditions, species richness converged in all cases to these expected values for a fully stochastic mid-domain model.

Extinction and speciation

Extinction was incorporated into the model by eliminating species whenever shifts in range limits produced the condition $L_2 < L_1$ for a given species. Thus, extinction was modelled as a process of range contraction to a final, single location. In our simple model, we assumed range cohesion and did not incorporate fragmentation as an extinction process. At the geographic scale, extinction can be examined empirically as a process of range contraction, either towards the centre or to the periphery (Channell & Lomolino 2000; Gaston 2003). The rule generated a process in which a constant proportion of species went extinct in equal time intervals. Thus, species disappeared following a negative exponential function with time ($S = S_0 e^{-mt}$), where S is the number of extant species, S_0 the initial number of species, t the time and m a constant, generating straight lines in the standard log(survivors) vs. time plots (Raup 1996; Fig. 3a). Extinction rate increased with increasing D values; thus, a higher rate of range movement increased the chance of ranges shrinking to a single point. When $D = 0.01$, for example, 84.2% of species survived each period of 1000 time steps, so after 30 000 time steps 0.57% of the initial number of species survived.

The number of extinctions was not constant along the latitudinal gradient. Instead, the proportional number of extinction events along the domain followed a second-degree polynomial function, $E = ax - ax^2$, where $a = 0.053$ and $R^2 = 0.723$, when computing the proportion

of extinction events at each point along the domain (Fig. 3b). This function has the same form as the equation for species richness in the fully stochastic version of mid-domain models ($S = 2x - 2x^2$; Colwell & Lees 2000).

To model speciation, in each time step and for each species, a barrier appeared with a constant probability O, at a random point along the domain. If the barrier lied within the range of a species, then the smaller derived segment was assigned to a new species and the larger segment to the parent species. Thus, allopatric speciation was modelled as a process of cladogenesis with survival of the parent species and origin of a new species at one edge of the original range. Although several other mechanisms of sympatric and allopatric speciation have been proposed in theory and documented in nature (Coyne & Orr 2004; Barluenga *et al.* 2006; Savolainen *et al.* 2006), allopatric speciation at the edge of a range is a reasonable process when analysing continental patterns of diversity and distribution (Barraclough & Vogler 2000; Chown & Gaston 2000; Waldron 2007).

We ran models including speciation but no extinction, setting $O = 0.001$ and starting with sets of 10 000 species located at random points along the domain. We ran a simulation for each species until a speciation event took place, recording the time to speciation and the point at which the event occurred. The frequency distribution of time to speciation followed a negative exponential function, so 26.4% of species had an origination event in the first 1000 time steps, whereas only 0.12% did not speciate until at least 19 000 time steps had passed (Fig. 3c). The propor-
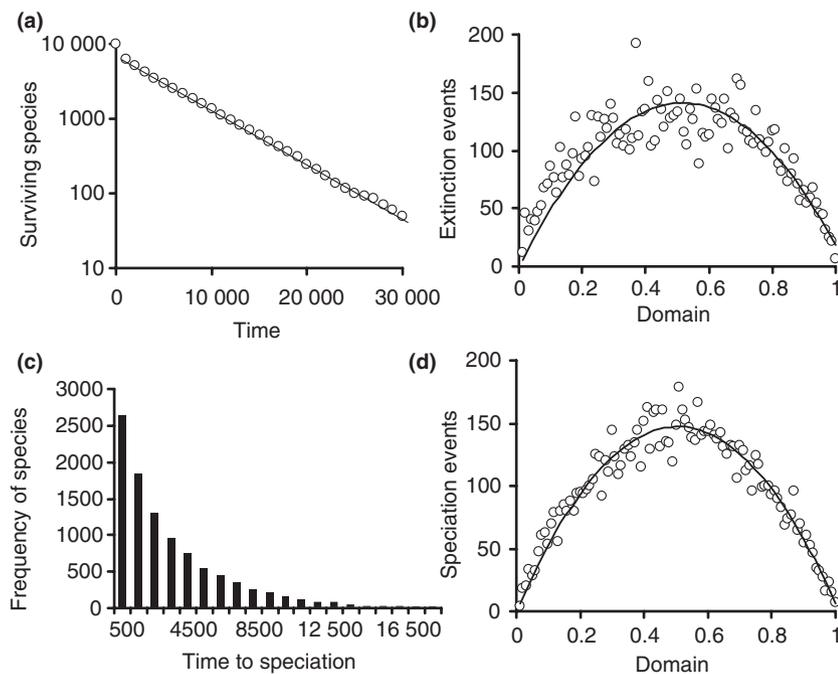

Figure 3 Extinction and speciation in sets of species with random-walk range dynamics. (a) Number of species surviving (from a set of 10 000 species) to different time steps in a model with no speciation. (b) Latitudinal pattern of extinction events in the model with no speciation. (c) Frequency distribution of time to speciation for a sample of 10 000 species in a model with no extinction. (d) Latitudinal pattern of speciation events in the model with no extinction.

tional number of origination events arranged along the domain following the equation $O = bx - bx^2$, with $b = 0.58$ and $R^2 = 0.93$ (Fig. 3d).

The interaction of speciation, extinction and range shifts

Our final model included range shifts, speciation and extinction, beginning with one species occupying the whole domain ($L_1 = 0.0$, $L_2 = 1.0$). We set only two parameters: D, defining the maximum movement of range limits at each time step, and O, the probability of the appearance of a barrier for a species at a given time step. Several combinations of D and O produced unstable cases in which all species went extinct or in which the number of species grew exponentially. Nevertheless, some combinations yielded simulations in which a steady state of species richness was reached after a period of increasing diversity (Fig. 4a). In all cases reported hereafter, we used $D = 0.01$ and $O = 0.035$, running the simulations for 30 000 time steps.

Figure 4a shows the diversification pattern of a typical run of the model. When the total number of species in the system was low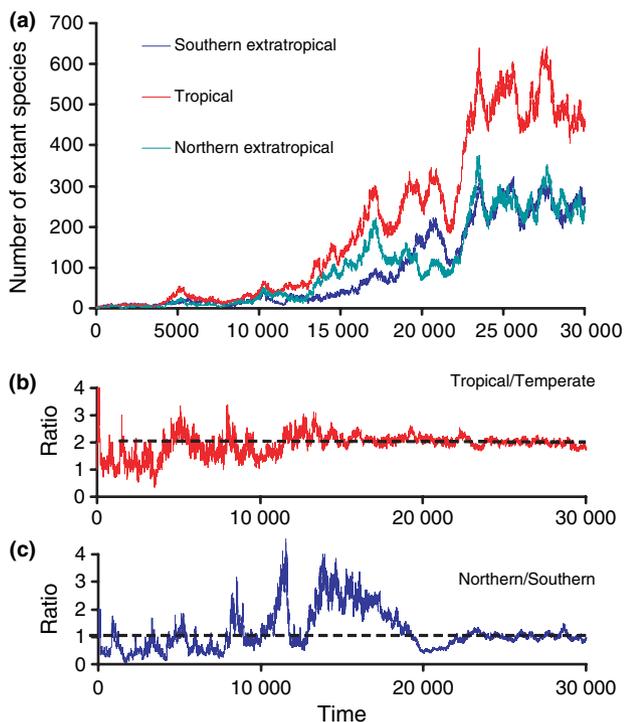 (< 100), such as in the first 10 000 time steps, the latitudinal pattern of species richness was very volatile, even showing episodes of a reversed gradient in which the average number of species was higher in the extratropical bands (Fig. 4b). As time passed and species richness reached a plateau, the latitudinal gradient stabilized towards a pattern in which the number of tropical species was about twice the average richness in each of the extratropical bands. For more than 20 000 time steps, the latitudinal gradient was asymmetrical, with the northern and southern bands alternating in sustaining a larger number of species. As species richness stabilized, however, the ratio of northern to southern extratropical species converged to 1 : 1, producing the final form of the latitudinal gradient of diversity (Fig. 4c).

With the data by species, we were able to refer every event of speciation (origination) and extinction to a particular time and position along the domain. The position of an origination event was that of the barrier that generated a new species, and the location of extinction was the point $L_1 = L_2$ where the southern and northern limits met, that is, the final location of a species just before its extinction. The cumulative number of speciation and extinction events was highest near the centre of the domain and lowest at both ends (Fig. 5). These patterns coincide with the ones of the simulations with no extinction and no speciation (Fig. 3b,d). The net rate of diversification (rate of origination minus rate of extinction, Jablonski *et al.* 2006) showed no latitudinal trend (Fig. 5a).

Species originating in the tropics were much more likely to go extinct within the tropical band and species originating in the extratropical bands were more likely to go extinct there (Fig. 5b). Cases in which a species originated in one of the extratropical bands and went extinct in the other extratropical band were very uncommon, as an obvious consequence of distance. In fact, in one run of the model that generated 40 596 species, 20 433 of them (50.3%) originated in the tropical band and 20 163 in one of the extratropical zones. Of the species with tropical origin, only 2023 went extinct in an extratropical band (9.9%), whilst 1687 species with extratropical origin (8.4%) went extinct in the tropics.

With the set of species that were not extinct after the 30 000 time steps, we examined parameters of 'modern biogeography', in the style of studies that rely on present-day patterns to reconstruct the evolutionary history of clades. The latitudinal pattern of species richness showed the hump-shaped pattern predicted by mid-domain models, but showing deviations produced by the stochastic nature of the model (Fig. 6a). Ranges were predominantly small, with no latitudinal extents larger than 0.4 units, so the frequency distribution of range sizes was highly skewed (Fig. 6b). Additionally, the absence of large ranges produced a plot of range size vs. position of
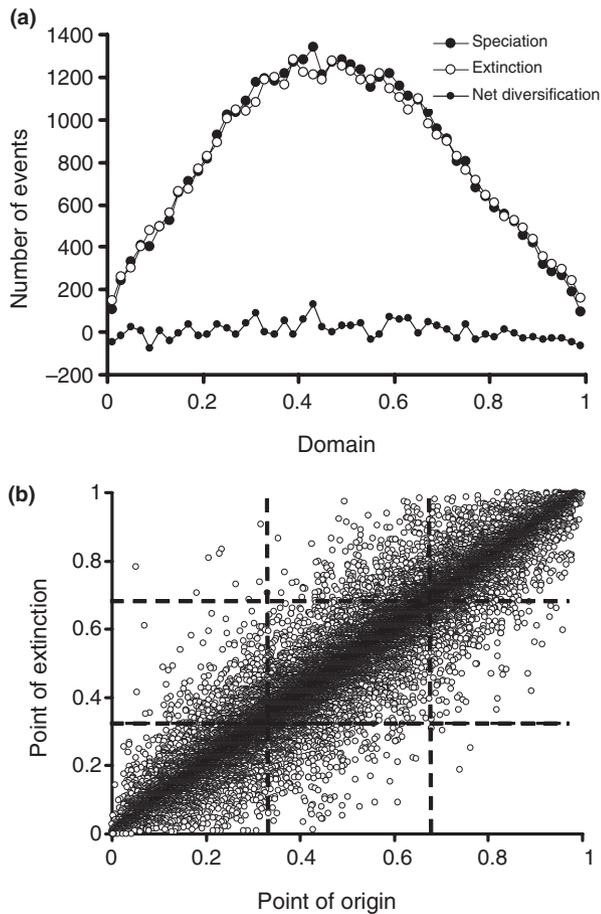

Figure 4 Temporal dynamics of richness for an assemblage of species with random-walk range shifts. (a) Species diversity in the three latitudinal bands defined in Fig. 2. (b) Dynamics of the ratio of tropical species diversity to average extratropical species diversity. (c) Dynamics of the ratio of northern extratropical species diversity to southern extratropical diversity.

(a)

(b)

Figure 5 Latitudinal patterns of speciation and extinction. (a) Total number of speciation events and extinctions along a latitudinal gradient for the simulation in Fig. 4. Net diversification is speciation minus extinction. (b) Extinction and origination point for 40 596 species generated by the simulation in Fig. 4. Lines mark the limits for the tropical and the two extratropical regions detailed in Fig. 2.

(a)

(b)

Figure 6 Age in the set of surviving species. (a) Correlation with range size. (b) Mean ± 1 standard deviation of age for species occurring at several points along the latitudinal gradient.

midpoint in which the triangle that contains the possible combinations of these variables was empty in its upper section (Fig. 6c).

We measured the age of species as 30 000 time units minus the time of origin and found a weak but significant correlation with range size ($R^2 = 0.09$, $n = 293$; Fig. 7a). To explore the relationship between latitude and age of species, we used two methods. In the first one, we calculated the mean and standard deviation of the age of species whose range intersected points along the latitudinal domain and found no apparent latitudinal trend (Fig. 7b). In the second one, we correlated the age of extant species with latitude (absolute distance from $x = 0.5$) of the midpoint of their present ranges and found no significant relationship ($R^2 = 0.002$, $n = 293$).
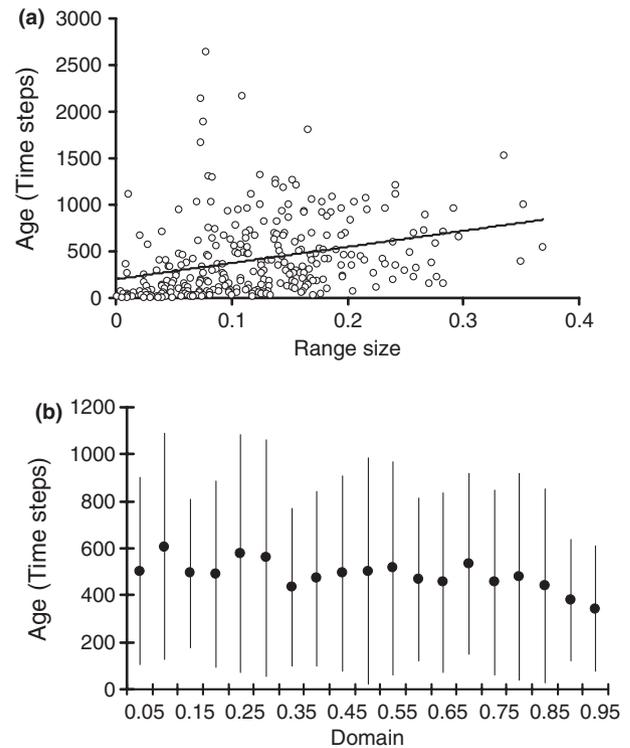
DISCUSSION

Null models and the dynamics of the latitudinal diversity gradient

Most evolutionary hypotheses that have been put forward to explain the latitudinal diversity gradient are variants of the time or the area hypotheses, or presume higher diversification rates in the tropics (Mittelbach *et al.* 2007). Simulations presented here constitute null models for both types of hypotheses as they model the diversification of a clade under a series of null conditions: (i) a domain of constant size and no environmental gradients; (ii) three equal-sized arbitrary regions with constant extent and no environmental differences between them; (iii) stochastic shifts of the borders of species' ranges, simulating non-deterministic, independent responses to random environmental changes; (iv) species with no defined niche traits; (v) no interaction among species, with ranges moving independently and (vi) no *a priori* latitudinal gradient in the rates of extinction and origination of new species.

The area hypothesis is based on the fact that the tropics have a larger surface of similar environments than any other part of the world. Therefore, according to the hypothesis, tropical species would tend to have larger ranges and
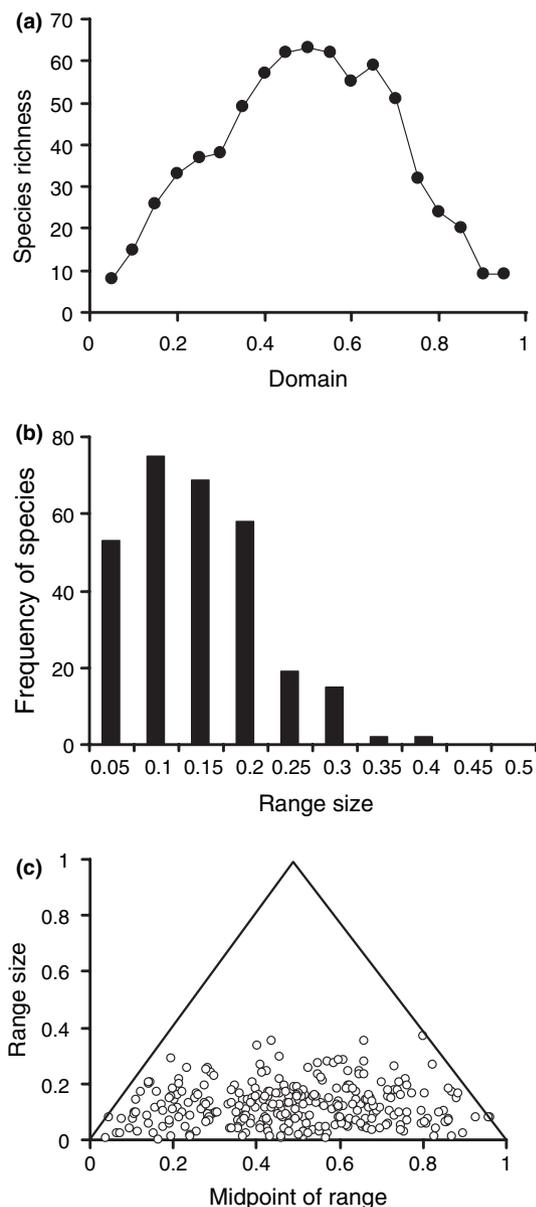
Figure 7 Species richness and range size in the set of surviving species. (a) Latitudinal gradient of species richness. (b) Frequency distribution of range size (latitudinal extent) among surviving species. (c) Plot of range size vs. position of the midpoint for the set of surviving species; the triangle encompasses the set of possible combinations of these two variables.

consequently higher rates of speciation and lower rates of extinction (Rosenzweig 1995; Chown & Gaston 2000). In our simulations, the latitudinal gradient was considered a continuum along which species' borders could move stochastically, so static gradients of environmental conditions were not defined. Additionally, our three latitudinal bands were defined arbitrarily to be of exactly the same size. Thus, simulations were, in principle, null to both aspects of

the area hypothesis (but see discussion on speciation rates below).

The time hypothesis incorporates the area effect into a temporal perspective. It postulates that the tropics have accumulated more species than temperate regions because larger areas with more constant environments have been available in the tropics over longer periods (Mittelbach *et al.* 2007). This is because temperate areas have sustained more pronounced climatic changes during the geologic history than the tropics, as shown for example by the Pleistocene glaciations, which have a strong influence on present-day patterns of species richness (Hawkins *et al.* 2003). The niche-conservatism hypothesis incorporates the idea that many clades that originated in the tropics have not had enough time to disperse to temperate regions (Wiens & Donoghue 2004; Wiens *et al.* 2006). Our model simulates the diversification of a large clade from a single species within a hard-bounded domain with fixed extent. As the three latitudinal bands were defined from the start of the simulations, and remained invariant, they had exactly the same available area for exactly the same time. Therefore, our simulations were also null to the time hypothesis.

We assumed no *a priori* differences in speciation or extinction rates between tropical and extratropical regions. Theoretical models and empirical data suggest that the rate of speciation is higher in the tropics because of the kinetic effect of higher temperatures on rates of genetic divergence (Allen & Gillooly 2006; Allen *et al.* 2006). Similarly, indirect evidence suggests that the rate of extinction in the tropics might be intrinsically lower than in temperate areas (Chown & Gaston 2000). The model presented here is null to these hypotheses, as speciation and extinction were set as stochastic processes with no *a priori* latitudinal pattern of occurrence.

Our model is also null to the different models that have been proposed for the dynamics of a species' range in terms of its size and position. These models include the age and area model (ranges steadily increasing in size), the cyclic model (the area model with fragmentation of ranges to generate new species with smaller ranges) and the stasis model (no size or position changes, Chown & Gaston 2000). Most models assume a strong influence of environmental factors in determining the changes in the position of the borders of ranges, but those shifts can be also the result of demographic responses determined by intrinsic traits of species, in turn shaped by natural selection (Holt *et al.* 2005). Recent studies have shown a consistent pattern of range dynamics in which ranges first increase in extent, reaching a peak size and then slowly shrinking to extinction (Foote *et al.* 2007; Liow & Stenseth 2007). Our model of range dynamics is null to all these models.

Finally, the model has no *a priori* definition of the range size of a given species or of any adaptations of that species

to particular environmental conditions. Therefore, our model differs from mid-domain effect models using 'spreading dye algorithms', in which the position of a species' range is defined by selecting a random point and filling adjacent areas in all directions until the empirical range size is attained, assuming a homogeneous one-dimensional domain (Lees *et al.* 1999), a two-dimensional homogeneous continent (Jetz & Rahbek 2001) or an environmentally heterogeneous continent (Rahbek *et al.* 2007). These models are not truly dynamic, because they do not simulate range expansions as biological processes. Instead, they use those expansions as an operational algorithm to set the location and shape of ranges. Dynamic models, in which the size, shape and location of ranges are determined by simulated evolutionary processes of extinction and speciation, have been recently developed (Rangel *et al.* 2007). These models, however, are intended to be predictive of present-day patterns of diversity and distribution by making explicit assumptions on niche conservatism of species, contrasting with our null approach of not considering any *a priori* niche trait for species. A truly dynamic null model, including range shifts, extinction and speciation, was recently developed for testing the idea of heritability of range size among related species (Waldron 2007).

Our simulations show that, even if null conditions prevail, a latitudinal gradient of species richness can be generated. Also, similar gradients develop for the rates of extinction and speciation, maintaining a steady-state dynamic equilibrium for the latitudinal gradient of species richness. The hump-shaped latitudinal pattern of extinction events arises due to statistical properties of random-walk processes. At each time step, L_1 and L_2 move a random distance (d_1 and d_2) in the interval $(-D, D)$. Thus, the net movement of the midpoint is $(d_1 + d_2)/2$, which also lies in the interval $(-D, D)$, but with higher probabilities for values close to zero than for the extremes (see Appendix S1 in Supplementary material). Therefore, after several time steps, the frequency distribution of possible end locations will be symmetrical with the highest probability at the starting point. In consequence, the most likely location for the extinction of a species is near the centre of its range. Interestingly, this effect takes place even if the hard boundary restriction is relaxed and the range limits can take any value, even outside the domain.

The hump-shaped latitudinal pattern of speciation, on the other hand, is due to a process related to the area hypothesis. A barrier randomly located along the domain has a higher probability of intersecting the range of a species if located near the centre of the domain. Additionally, larger ranges will have higher probabilities of being intersected than smaller ranges. Thus, 'tropical' species with larger ranges will have higher probabilities of generating new species, just as the area hypothesis predicts. However, the area hypothesis also assumes that, for biological and geographic reasons, tropical species should have larger ranges because larger extents of suitable habitats are available near the equator. In contrast, our model makes no such assumption, and the area effect on speciation rates arises because of statistical and geometric constraints. In a similar vein, our model does not predict, as the area hypothesis does, a lower extinction rate in tropical areas.

Insights from extant species

Stochastic dynamic models of diversification can be used as null models for reconstructions of evolutionary history from present-day patterns of diversity and distribution (Waldron 2007). Predictions of our model differ in the details from those of the fully stochastic mid-domain model (Fig. 6). The number of surviving species showed the typical hump-shaped curve along the domain predicted by mid-domain models (Fig. 6a), but the frequency distribution of range sizes and the relationship between range size and midpoint position showed important deviations, determined by the absence of species with very large ranges, whose formation and long-term viability were precluded by the speciation process of our model (Fig. 6b,c). The range-size frequency curve was more similar to empirical distributions than the linearly decreasing pattern predicted by the fully stochastic mid-domain model (Colwell & Lees 2000; Arita 2005), although in our model the smallest sizes were underrepresented as well (Fig. 6b). Similarly, the upper sector of the triangle of possible range-size midpoint values was empty due to the absence of large ranges (Fig. 6c).

We found a significant correlation between the range size of surviving species and their age (Fig. 7a). This pattern, when found for empirical data, has been interpreted in two different ways: (i) that species with larger ranges are inherently less susceptible to extinction or (ii) as a demonstration of the age and area hypothesis, which predicts a steady increase of range size as species get older (Jablonski & Raup 1995; Webb & Gaston 2000). Our model shows that such correlation can be generated by stochastic range shifts alone, without invoking any kind of biological process.

A recent study found negative correlations between midpoint latitude of range and age of New World bird and mammal species (Weir & Schluter 2007). Based on a birth–death model simulating gradients of extinction and origination, a higher temporal turnover of species at higher latitudes was invoked as an explanation for these patterns. Our simulation is a null model for these results. We found that, under stochastic dynamics, range location of surviving species is not correlated with their age, and that there is no latitudinal trend in the age of species, so a mechanistic

explanation for the empirical patterns found for birds and mammals is warranted. Our simulations also show, however, that the pattern of no latitudinal gradient in age can be generated even with a higher temporal turnover of species in the tropics. Thus, predictions of pure birth–death models that ignore shifts in the ranges of species should be taken with care when interpreting present-day patterns of diversity.

Tropical cradles, museums and casinos in real and null worlds

Predictions of our model do not conform well to any of the existing general models of tropical diversification (Fig. 1). Simulations yielded a pattern in which both extinction and speciation rates are higher in the tropics; that is, a more intense temporal turnover of species in the tropics, but no significant latitudinal variation in net diversification rates (Fig. 5a). The tropics would be a cradle of diversity, but hardly a good museum (Stenseth 1984).

If speciation and extinction patterns alone cannot fully explain the latitudinal gradient of diversity, dispersal must play a significant role (Goldberg et al. 2005; Jablonski et al. 2006; Roy & Goldberg 2007). The stochastic model generates processes that are contrary to those proposed by the 'out of the tropics' hypothesis, which postulates a tropical origin for most clades, with a net dispersal to temperate areas (Jablonski et al. 2006). In our simulations, dispersal into the tropics can by itself generate the latitudinal gradient of diversity, as a consequence of the mid-domain effect (Fig. 2b). Stochastic dispersal, combined with random processes of speciation and extinction, generate strong latitudinal gradients of diversity (Fig. 4) and particular patterns for surviving species (Figs 6 and 7). Only a small proportion of species originating in the tropics disperse to extratropical areas, and in fact a very high percentage go extinct within the tropical band (Fig. 5b).

It is important to emphasize that we do not consider the simulations presented here as predictive models for the evolution of diversity. Rather, we envision the results of our simulations as null expectations of how the patterns of diversity would conform in the absence of many important biological processes, such as species interactions and the effect of climate. Thus, we view our models from a 'weak' perspective (Bell 2001), and use them to generate a null hypothesis against which results from empirical studies or from predictive models can be compared. A 'hard' version of our model would presume that the processes involved in the simulations (stochastic range shifts and speciation) are the actual mechanisms that have generated the patterns that we see in present-day species assemblages (Bell 2001). For example, global data for marine bivalves of the last 11 million years support the out of the tropics model

(Jablonski et al. 2006), showing higher rates of origination and lower rates of extinction in the tropics, and a tendency of tropical taxa to disperse to extratropical areas. Because these data do not conform to the predictions of our model, a 'hard' interpretation would postulate our simulations to be a competing mechanistic explanation against the out of the tropics theory. In contrast, in our 'weak' view, differences between the empirical observations of Jablonski et al. (2006) and our null predictions might mean that non-random biological mechanisms are likely to govern the dynamics of marine bivalve diversity. As pointed out by Gotelli & McGill (2006), if models akin to the neutral theory are used as statistical null hypotheses (H_0), then an appropriate alternative hypothesis (H_A) must be specified. For our models, alternative hypotheses can include the effects of species interactions, of past or present-day climate, or of time and area.

As in classic null models, all species are treated in our simulations as independent, non-interacting entities. In our model, even the two borders of a species' range respond independently to stochastic environmental changes. In contrast with traditional null models, ours is dynamic. One-dimensional mid-domain models have simulated diversity and distribution by randomly locating the ranges of species along a homogeneous domain. The size of ranges in these models is determined either randomly or by sampling from an empirical frequency distribution (Colwell & Lees 2000). Thus, classic mid-domain models generate statistical null hypotheses (Bell 2000; Gotelli & McGill 2006). In contrast, our model generates dynamic null hypotheses by incorporating a stochastic component through the simulation of random-walk shifts in the ranges of species. Our model resembles the fully stochastic version of the mid-domain model (Colwell & Lees 2000) in determining the range size of species through a random procedure. However, the procedure is static in the classic mid-domain model and dynamic in our simulations.

The dynamic nature of the range of species is a recognized fact (Gaston 2003), but the inherent difficulties in inferring shifts in the ranges through geological time from the fossil record has precluded detailed studies on the subject and has hindered the development of theoretical models (but see Gaston & He 2002; Holt et al. 2005; Liow & Stenseth 2007). We have shown that very simple stochastic models of range shifts, with very few biological assumptions, can generate complex patterns of diversity, similar to those found in nature. Thus, these null models should be considered when testing hypotheses regarding the origin and maintenance of biological diversity. Range dynamics and stochastic processes should be taken into consideration in any discussion on tropical cradles or museums.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Extinction in the one-dimensional random-walk model of range dynamics.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01197.x

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