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The mid-domain effect: geometric constraints on the geography of species richness

Robert. K. Colwell and David C. Lees

Geographic patterns of species richness are influenced by many factors, but the role of shared physiographical and physiological boundaries in relation to range-size distributions has been surprisingly neglected, in spite of the fact that such geometric constraints lead to mid-domain richness peaks even without environmental gradients (the mid-domain effect). Relying on null models, several recent studies have begun to quantify this problem using simulated and empirical data. This approach promises to transform how we perceive geographic variation in diversity, including the long unresolved latitudinal gradient in species richness. The question is not whether geometry affects such patterns, but by how much.

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The latitudinal gradient in species richness, perhaps the most conspicuous feature of global biogeography, has intrigued ecologists and biogeographers continuously since the times of de Candolle (Ref. 1, pp. 1270–1276) and Wallace (Ref. 2, pp. 65–68). In spite of this long history, consensus on the causes of tropical peaks in species richness remains elusive[3–5]. The overwhelming range of hypotheses proposed to account for changes of species richness (Palmer[6] lists 120 named hypotheses for variation in species richness or coexistence, and Rohde[7] identifies 28 specifically applied to the latitudinal gradient) makes the task of sorting out which factors are causal and which are incidental a daunting one. Increasingly, using computationally intensive methods, ecologists and biogeographers are looking for answers at a regional or a global scale, putting models and hypotheses[7–15] to the test against increasingly comprehensive distributional data encompassing the still poorly known tropics[15–19].

This search has taken an unexpected turn. In spite of the plethora of climatic, ecological, evolutionary and historical explanations proposed to explain biogeographic diversity patterns, something fundamental has, until recently, been almost completely ignored: the geometry of species ranges in relation to geographical boundaries. Based both on simulations[11,12,14] and on analytical null models[13,15], it is now clear that a mid-domain peak or plateau in species richness is inevitable for virtually any set of ranges, theoretical or empirical, when these ranges are randomly placed within a bounded geographical domain, in the complete absence of any supposition of environmental gradients within the domain. Qualitatively, this result survives a wide range of changes in model details and assumptions. Quantitatively, it explains a surprisingly large proportion of geographic variation in species richness for diverse groups of organisms, for the empirical cases so far examined. In spite of conceptual antecedents in the ecological literature dating back more than 40 years[20], and a substantial literature on formally analogous problems in niche overlap and phenology (Box 1), this important result seems to have gone unnoticed until 1994 (Ref. 11).

What do the geometric models predict?

There is a growing consensus that the regional pool of species is the key determinant of the species composition of more or less unsaturated local communities[21,22]. Based on regional biotas, geometric models[11,13–15] demonstrate that the stochastic placement of species ranges between shared geographic boundaries can generate precise predictions of species richness at points between the boundaries. For example, in the case of random, one-dimensional placement of ranges between two boundaries, the null models predict a convex, symmetrical pattern of species richness: this pattern is either parabolic[11,13] or quasi-parabolic[11,15] depending upon alternative distributions of range sizes and of midpoints (Fig. 1; Boxes 2 and 3). An instructive way to grasp this idea quickly is to experiment with a null model that simulates range size and randomizes range placement within differently defined boundaries[11] (Fig. 1). (A graphical simulation program, that not only implements the principal stochastic range model variants, but also allows input of empirical range-size frequency


Box 1. Antecedents and analogues

The species range has long been studied as the fundamental unit of species richness gradients[29–33]. Although some modeling approaches have incorporated aspects of range size evolution, distribution or overlap[29,34–37], species richness has traditionally been viewed as a function of area, history and climatic or biological gradients, rather than geometric constraints. Colwell and Hurtt[11] were apparently the first to show that mid-domain species richness peaks can arise from geometric constraints alone, although analogous problems in ecology have been studied for more than 40 years.

In his classic paper on the relative abundance of species, MacArthur[20] proposed two 'broken stick' models. The first of these (*n* independent, uniform random breaks in a single unit 'stick', producing *n* + 1 pieces) became the focus of much further attention (e.g. May[38]) – notwithstanding MacArthur's attempt to bury it[39]. MacArthur's second model was a random, 'overlapping niche' model: two independent, uniform random hits to the unit 'stick' defined the endpoints of each species (*n* pairs of points for *n* species). However, in spite of the niche overlap metaphor, MacArthur was concerned only with the distribution of the length of the pieces, not the patterns of overlap among them along the unit line. Quickly dismissed for its poor fit to relative abundance distributions, the two-hit broken stick model was resurrected by Pielou[40,41] (and Dale[42,43]) to assess the randomness of distributional overlap among species along gradients. Later, Pielou extended this approach, theoretically and empirically, to an analysis of latitudinal overlap among congeneric seaweed species[31,36,37]. But neither MacArthur nor Pielou examined the expected distribution of range overlaps as a function of location on the domain; thus, they failed to discover the mid-domain peak of richness.

The overlap of phenological events within a temporal domain is precisely analogous to (one-dimensional) geographical range overlap within a spatial domain. To test for non-random spacing of flowering periods, Cole[44] and others (reviewed by Gotelli and Graves[45]) computed expected pairwise overlaps and randomized empirical flowering periods within the flowering season. Cole[44] and Sugihara[46] extended Pielou's[41] analytical approach to phenology and to utilization spectra in general. Nonetheless, no one in the phenology debate examined the expected number of simultaneously flowering species as a function of time of year for randomized flowering periods, for which the mid-domain effect predicts a mid-season flowering peak.

Perhaps the most obvious manifestation of geometric constraints on patterns of geographic range on a bounded domain is the limitation placed on the relation between range size and range midpoint (Fig. 1b). Species with midpoints near a boundary necessarily have relatively small ranges or, conversely, species with increasingly larger ranges must have their midpoints increasingly nearer the centre of the domain. Pielou[31,37] was apparently first to recognize (and plot) this constraint, followed by Graves[47] (elevation), Rhode *et al.*[48] (latitude), and Pineda[27] (depth). Although their contributions pointed out the boundary constraint on range placement – ultimately the cause of richness peaks in stochastic range models – none of these authors noted the expected mid-domain peak.
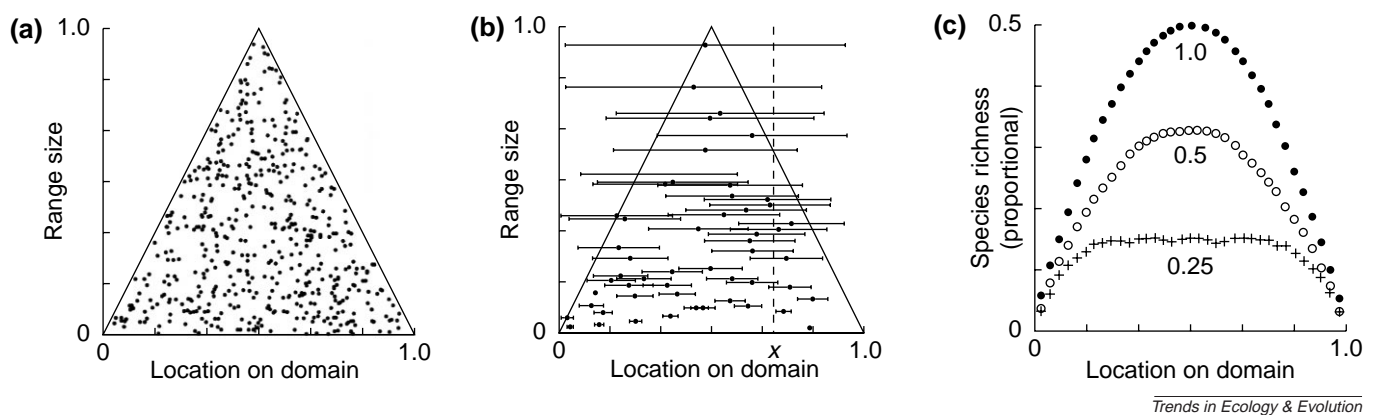
Fig. 1. A fully stochastic null model for species richness gradients within a bounded domain[11]. For particular sets of species, the unit domain might represent elevation from sea level to mountaintop[16], ocean depth from the surface to the abyss[14], distance from one end of a large island to another (Fig. 3), latitude from the northern to the southern end of the continental New World (Fig. 2a), or latitude from the northern to the southern limit of the distribution of a clade (Fig. 2b). In (a), the range size for each species is plotted against its range midpoint (500 species shown). In this model (Box 2), midpoints and range values are generated as a uniform random coverage of feasible values. In (b), the ranges for a subset (50 species) of the points in (a) are shown as horizontal lines centred on their midpoints. Because the domain is bounded at 0 and 1, all midpoint-range coordinate pairs – the points in (a) and (b) – must lie within the isosceles triangle. For any point *x* in the domain, richness is computed as the number of horizontal range lines that a vertical line at *x* (the broken line) would intersect. In (c), the closed circles show the pattern of species richness across the domain for the points in (a) and (b). The open circles plot species richness when maximum range size is limited to half the domain (0.5) and the crosses show richness for a maximum range size of 0.25. The ordinate in (c) scales richness as a proportion of all species in the simulation. In all cases, the richness peaks at the domain midpoint. Only the top curve is parabolic and peaks at a proportional richness of 0.5. Note the more pronounced mid-domain effect when larger ranges are permitted. *Modified, with permission, from Ref. 11.*

distributions and exports the results, is freely downloadable from the web – http:// viceroy.eeb.uconn.edu/rangemodel). To date, two analytical versions of the one-dimensional geometric model have appeared (Boxes 2 and 3)[13,15]. The first of these[13] generates (with confidence intervals) the predicted species richness for the fully stochastic interaction of range size versus range midpoint within predefined boundaries; the second[15] supports analytical estimation of expected species richness, based on empirical range-size frequency distributions, and extends the approach, tentatively, to two dimensions.
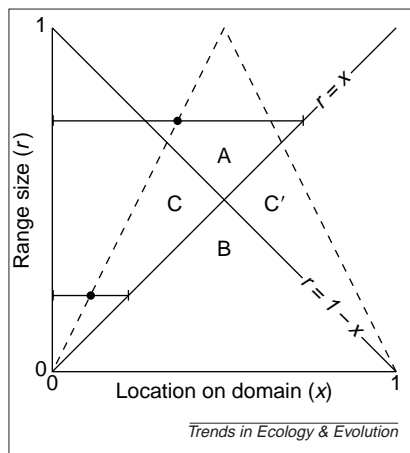
The richness gradient predicted by the geometric models certainly matches, in its bilateral symmetry and its unimodality, the latitudinal patterns of species richness documented for most higher taxa[11,13]. The models explain a remarkably high proportion of empirical variation in latitudinal richness for some taxa[13] (Fig. 2). A striking prediction of these models is that richness patterns on elevational gradients and on bathymetric gradients should also be unimodal, with a mid-gradient richness peak[11,14,15]; this prediction of a mid-gradient richness peak defies the longstanding dogma[23] that species richness decreases monotonically with increasing elevation and depth[24,25]. In fact, most data and recent meta-analysis suggest that richness patterns with a medial peak might be more the rule than the exception for both the elevational gradient[15,16,23,26] and the bathymetric gradient[14,27], although the

Box 2. A fully stochastic null model for species richness gradients

Model 2 of Colwell and Hurtt[11] is, in essence, a fully neutral model. No assumptions are made as regards range size and range placement, except for the geometric constraints of boundaries. This model is fundamentally equivalent to the two-hit broken stick model of MacArthur[20] described in Box 1, and the binomial model of Willig and Lyons[13].

To demonstrate this equivalence and to relate this model to the others in Box 3, the probability of intersecting a geometrically constrained line segment generated by chance alone was sought[13]. This is the unconditional probability $p(x,r)$ that a range of size r overlaps a sampling point at x, where x is any point within the domain (Fig. 1b). According to Bayes' Theorem, $p(x,r) = p(r)$ $p(x|r)$. The distribution of range sizes determines the probability $p(r)$. For a random uniform distribution of midpoint densities within the midpoint constraint triangle, as shown in the figure here, $p(r)$ is a linear decreasing function of range size, $p(r) = (2-2r)$ (Fig. 1b)[11,20]. We know the conditional probability $p(x|r)$ from the Lees model[15] (Box 3) for the triangular areas in the plot of r against x figured here. (The bars represent two different ranges at their leftmost positions.) The two diagonals $x = r$ and $x = (1-r)$ bound an hourglass-shaped region where $p(x|r)$ is maximal for the two triangles {A, B} as {1, $r/(1-r)$}, whereas for {C, C'} $p(x|r)$ increases with x up to these diagonals as {$x/(1-r)$, $(1-x)/(1-r)$}[15]. We next transform the r axis to the range size distribution for this model by applying the inverse of its ranked distribution function $(2r-r^2)$ (Refs 11, 20), which is $[1-(1-r)^{0.5}]$ (Ref. 11). We then integrate, for any value of x, the range intersection probability densities resulting from the product of $p(r)$ and $p(x|r)$ for {A, B, C, C'} in the figure, namely {$2-2r$, $2r$, $2x$, $2-2x$}. These values increase towards one at the intersection of $x = r$ and $x = (1-r)$. The integral for this distribution of r evaluates to $2x-2x^2$, a true parabolic curve describing proportional species richness.

(Online Fig. I)

This is precisely the same result that Willig and Lyons[13] elegantly derived using a binomial model. Suppose two points placed at random on a unit domain define the endpoints of a species' range. (This is exactly the 2-hit broken stick model of MacArthur[20], discussed in Box 1.) Now consider a sampling point x on the domain. Then the proportion of ranges for which both endpoints of the range fall to the left of x is x^2 and the proportion falling to the right of x is $(1-x)^2$. Therefore, the proportion that actually intersect the sampling point is $1-x^2-(1-x)^2 = 2x-2x^2$. From this result, the expected peak proportional richness at mid-domain for this model is 0.5, as shown mathematically by Willig and Lyons[13] and graphically by Colwell and Hurtt[11].

Box 3. Constrained null models for species richness gradients

In addition to the fully stochastic model discussed in Box 2, we can distinguish two other fundamental geometric null models for one dimension, constrained according to the dependence structure of either range size or range placement. These correspond to the model of Lees et al.[15] and Model 3 of Colwell and Hurtt[11]. As for the fully stochastic case (Box 2), each of these two models generates a convex, symmetrical pattern of species richness owing to the mid-domain effect, differing only quantitatively. (The simulation program of Colwell implements all three models: http://viceroy.eeb.uconn.edu/rangemodel)

The model of Lees et al.[15] effectively randomizes range placements given range sizes. This probabilistic, analytical null model assumes a uniform distribution of range sizes, but can be partitioned to approximate empirical range size distributions (see Box 5). Here, we seek $p(x|r)$, probability densities derived[15] for the triangles in the figure in Box 2, whose integration for this distribution of r evaluates to the proportional species richness function:

$$-(1-x)\ln(1-x)-x\ln(x)$$

This describes a quasi-parabolic curve whose peak at $x = 0.5$ takes the value ln(2), or about 0.69 of the total species pool endemic to the domain. Pineda and Caswell[14] introduced a Monte Carlo version of the same model.

The second constrained geometric null model (Model 3 of Colwell and Hurtt[11]) is based on ranges drawn at random from geometrically feasible values for a given range midpoint (although left or right endpoint could just as well be used). In this case, we seek $p(x|m)$. With a uniform random distribution of midpoints (as in Colwell and Hurtt's Model 3), this model generates a hollow-curve range size frequency distribution that seems biologically quite realistic[35], but produces a build-up of particularly small ranges towards the domain boundary, where ranges are allowed only a small amplitude[11]. As indicated graphically by Colwell and Hurtt[11], the expected peak proportional richness for this model (for a proportional maximum range size value of unity) is approximately 0.3, with a medially rather flattened, quasi-parabolic, species richness curve. Pineda and Caswell[14] also used this model in its Monte Carlo form. No analytical version of this model has yet appeared.

richness peak is often not precisely in the middle of the gradient.

Another pattern predicted by the models (but in this case predicted by no other hypothesis) is that, regardless of latitude, the richness of terrestrial groups should peak in the middle of large, isolated, continuous biomes to which they are endemic, as a result of the constraints imposed by biome boundaries. Lees et al.[15] documented a striking confirmation of this prediction for Madagascan rainforest (Fig. 3).

Naturally, boundaries vary in their potential to limit species distributions. For example, mountaintops set absolute elevational limits for non-airborne organisms, and land–sea limits fortified by deeper ocean trenches offer strong resistance to range expansion within most terrestrial clades. Other limits might be more yielding. Lyons and Willig[12] included physiological frontiers along with topographic features, such as orographic barriers, in the category of 'soft' boundaries; whereas Colwell and Hurtt[11] used 'hard' to refer to any naturally definable biogeographic barrier that presents some degree of resistance to dispersal. Thus, defining, quantifying or even ranking barrier resistance is likely to remain a challenge, because the effectiveness of boundaries depends greatly on the temporal scale on which they are considered and on the phylogenetic constraints. At least, physiological limits to the geographic distribution of a clade might be just as effective as sharp physiographical boundaries on the shorter time scales most relevant to macroecological patterns[28].

The ongoing debate over Rapoport's rule[8] and the idea that the evolution of broadened physiological tolerance favours larger range sizes towards the harsher extremes of environmental gradients have motivated much of the recent work discussed here. The relationship between Rapoport's rule and the geometric models is complex (Box 4), but the models clarify the constraints on range size variation within domains and highlight the limitations of Rapoport's rule as an explanation for richness patterns.

The mid-domain effect: a geometry of ranges and richness

We call the geometric theory of species richness gradients the 'mid-domain effect'. We define the mid-domain effect as 'the increasing overlap of species ranges towards the centre of a shared geographic domain due to geometric boundary constraints in relation to the distribution of species' range sizes and midpoints'. Here, we place the limits of a
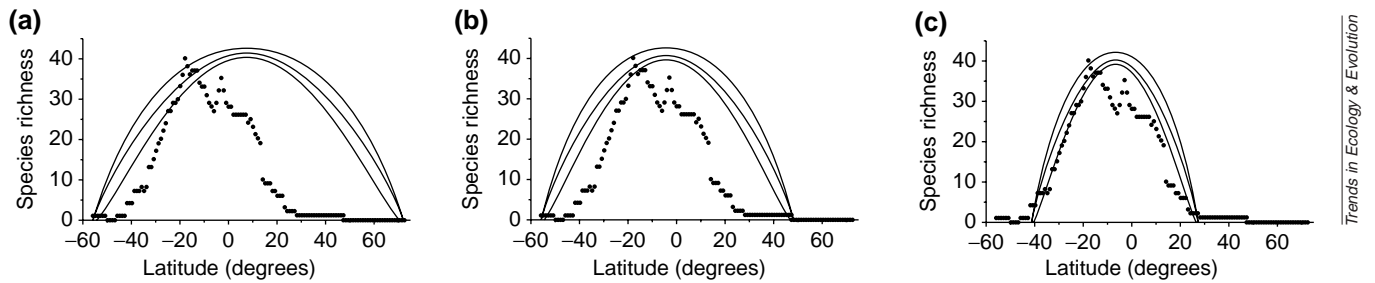
Fig. 2. Comparison of actual latitudinal patterns of species richness for New World marsupials (points) with patterns predicted by the fully stochastic null model[10] (solid curves) (Fig. 1; Box 2). In each graph, the central curve represents the predicted mean richness for each latitude; the outer lines define the 95% confidence bands. The same empirical data points are shown, with model predictions, for three different latitudinal domains: (a) the continental New World, (b) the distributional limits of all New World marsupials and (c) the smallest domain within which 95% of all New World marsupial species occur. *Reproduced, with permission, from Ref. 13.*

domain (in its mathematical sense of a union of a connected set and its boundary points) in a geographic context, either physiographically (e.g. the land–sea interface[14]), biologically (e.g. biome interfaces, such as tree-line or the limits of rainforest in Madagascar[15]), as the limits of a region of endemism (e.g. the northern and southern range limits of New World marsupials[12]) or arbitrarily (e.g. 20°N to 20°S latitude). Although we focus on one-dimensional views of geographical domains and their geometric representation on a line, the concept applies equally to geographical areas and to volumes. Although clearly related to earlier models of geometric constraints (Box 1), the mid-domain effect focuses on the emergent, macroecological pattern that these constraints predict, rather than on the effects of constraints on individual ranges. (The effect has also been referred to, without explicit definition, as the 'geometric constraint model'[14] or 'the Périnet effect'[26]).

In assessing the role of the mid-domain effect in specific cases, an important element of this definition is that the species considered must, collectively, share the same boundaries. In other words, species ranges that are not fully contained in the geographical domain under consideration are excluded (although such taxa can still be analysed using different domain limits). The resulting shape, intensity and, thus, detectability of the mid-domain effect depends on the taxa involved; the distribution of their range sizes and range midpoints; the existence, location and limiting potential of the boundary constraints; the sampling position or region; and on countervailing or intensifying biological, climatic or historical determinants of species richness. Thus, confirmation or rejection of the mid-domain effect in any particular case requires statistical evaluation of an appropriate null model in relation to observed patterns[13–15].
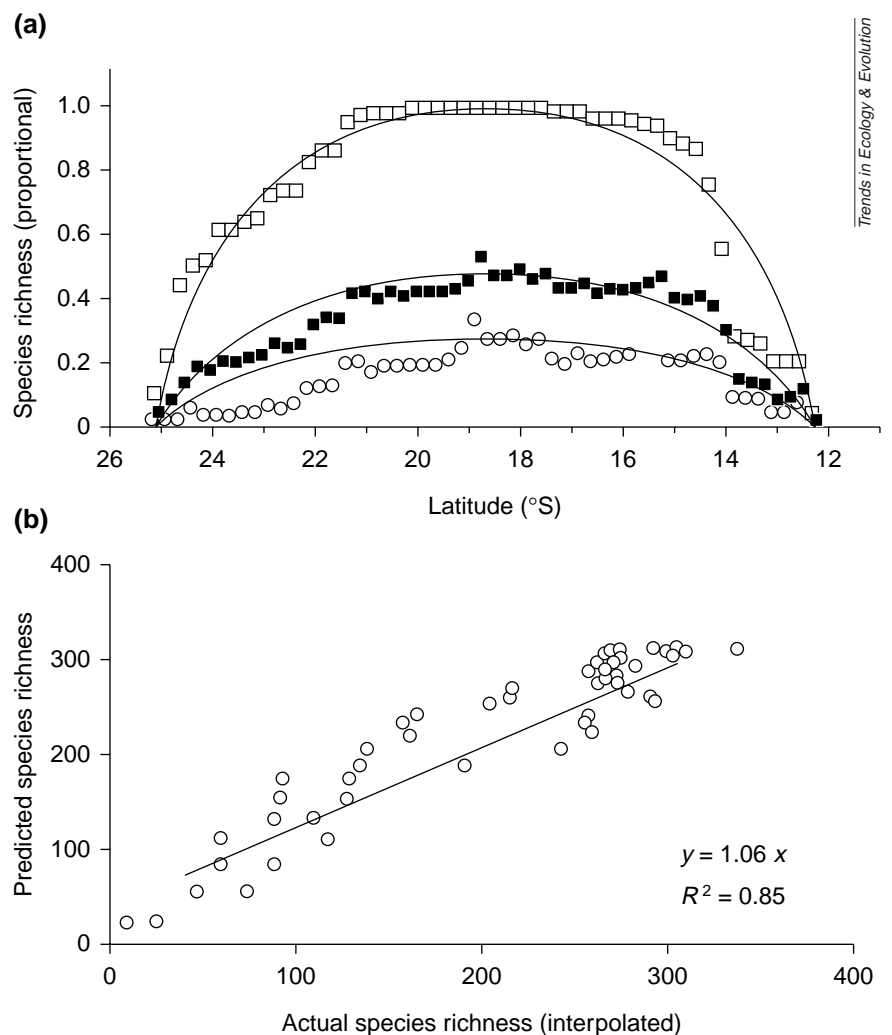
Fig. 3. Latitudinal proportional species richness, based on interpolated ranges, for species strictly endemic to the Madagascan rainforest biome[15]. In (a) observed richness for ten faunal groups (enariine beetles, tiger beetles, butterflies, ctenuchiine moths, chameleons, frogs, birds, tenrecs, rodents and lemurs) is compared with an analytical null model (Boxes 3 and 5). The model computes expected richness based on either two or four equal partitions of range size[15]. The middle curve represents all 637 species (closed squares, observed; solid curve, 4-partition analytical model). The top curve represents all 182 wide-ranging species – species with ranges that cover at least half the domain (open squares, observed; solid curve, 2-partition analytical model). The lower curve represents all 455 narrow-ranging species – species with ranges that cover at most half the domain (open circles, observed; solid curve, 2-partition analytical model). *Modified, with permission, from Ref. 15.* In (b) the same data are plotted as for the middle curve in (a) for all 637 Madagascan rainforest species, showing the fit to 4-partition analytical geometric null model, which explains 85% of the variance (uncompensated for spatial autocorrelation).

Box 4. The geometric models and Rapoport's rule

Following Rapoport[32], Stevens[8] reported greater average latitudinal range among species at higher latitudes, for certain taxa, a pattern he called Rapoport's rule. Extending the idea to both elevational[24] and bathymetric[25] richness gradients, based on an analogy between low latitudes, low elevations and shallow waters (and their opposites), Stevens supposed a monotonic decrease in richness (now called into question for both elevation and depth[14–16,23,26,27]) and increasing average range size at higher elevations and greater depths[49]. Stevens[8,24,25] also proposed that narrow ranges in tropical, low elevation and shallow-water communities might actually cause high richness by the spill-over or mass effect of Schmida and Whittaker[50]: a hypothesis that Stevens termed the Rapoport rescue effect.

Geometric constraints complicate any consideration of Rapoport's rule[11,12,17,27]. Colwell and Hurtt[11] showed that incorporating the boundary constraint in two basic null models of range size versus range midpoint (Boxes 2 and 3) produces a pattern of average range size across a domain that is either flat or opposite to that predicted by Rapoport's rule. Lyons and Willig[12] went further, arguing that a valid test of Rapoport's rule ought first to account for an expected negative correlation between latitudinal range midpoint and range size forced by the boundary constraint[27,44,47]. Using bounded null models to assess this correlation for New World bats and marsupials, they showed that average range size for these groups does indeed decline with latitude (opposite to Rapoport's rule) but declines less than predicted by the null models. Although Lyons and Willig[12] suggested that this result is 'in the spirit of Rapoport's rule', such a pattern certainly does not support Stevens'[8] mechanism for high tropical species richness, which invokes absolutely smaller ranges among tropical species than among species at higher latitudes.

By contrast with the two Colwell models, the Lees model[15] (Box 3) produces a pattern consistent with Rapoport's rule. Lyons and Willig's[12] observation that boundary constraints force a steady decrease in range size as range midpoints become closer to a boundary (e.g. at high latitudes), in opposition to Rapoport's rule, is complicated by the interaction of differing range size distributions with boundaries[11]. Whether the final Rapoport curve is concave (standard), flat or convex (reversed) depends upon the range size frequency distribution. Random placement of ranges drawn from theoretical or empirical size frequency distributions with a higher proportion of large ranges (such as the Lees model, which assumes a uniform distribution of range sizes) can produce a standard Rapoport effect, whereas range size distributions with a preponderance of smaller ranges tend to yield a reverse effect.

Ironically, high richness at domain centres is disproportionately the result of any wide-ranging species, regardless of whether they predominate in a particular model[11,14,15,49]. Likewise, enforcing a gradient of increasing average range size towards high latitudes, in accordance with Rapoport's rule, generates a reverse latitudinal richness gradient, even without boundary constraints, because of increased overlap of wider-ranging species at high latitudes[11,49]. Finally, Rapoport's rule and the geometric models make entirely different predictions about richness gradients and their causes on elevational and bathymetric transects[11,14], because geometric constraints predict mid-domain richness peaks, which Rapoport's rule alone cannot do.

Box 5. Evaluating the mid-domain effect for empirical range size distributions

The constrained models of Box 3 have been extended to empirical distributions of range sizes and of midpoints. For the empirical version of the constrained range-size model, two approaches have been taken to shuffle empirical range size distributions. Both assume a uniform distribution of midpoints, within boundary constraints. Lees' approach, an analytical method based on partitioning of range sizes, integrates the probability densities shown for the figure in Box 2 between the relevant limits of r for each range size class, then weights the result by the proportion of species in each class, before summing these terms[15] (Fig. 3). In the second, Monte Carlo approach, the empirical distribution of range sizes is sampled and each sampled range is placed on the domain at random, given the midpoint constraints imposed by the size of the range. The simulation program of Colwell (http://viceroy.eeb.uconn.edu/rangemodel) implements this approach for empirical range sizes; the simulations of Pineda and Caswell[14] (their Figs 5 and 6) use a similar method for range placements. In an empirical version of the constrained midpoint model, Lyons and Willig[12] (in their 'pseudorandom' simulations) assigned a range at random, within boundary constraints, to each empirical midpoint. We suspect that incorporating both empirical range size and range placement distributions into a geometric null model would produce a model so constrained that statistical comparison with empirical richness patterns would have little power to reject a false null model[45]. Evaluation of the fit of these null models to corresponding empirical data should include not only comparison of predicted and observed richness patterns on the domain[13–15], but also comparison of patterns of midpoint placement (when ranges are constrained) or range size distributions (when midpoints are constrained).

The methodology for empirical tests needs much further work, especially in devising ways to separate the mid-domain effect (inevitably present) from biological and historical causes of richness peaks. The challenge of applying fully analytical two- and three-dimensional geometric null models to quantitative biogeographical patterns still remains, although Taylor and Gaines[51] simulated two-dimensional ranges on a sphere. As an approximation, Lees et al.[15] produced a two-dimensional, geometric species richness map by iterating the one-dimensional, analytical null model of Lees (see above) along the smaller (longitudinal) axis, given regional latitudinal range size frequencies. The history of null models in other areas of ecology[45] suggests that no single null model for the mid-domain effect will be, or should be, declared the 'correct' one. Rather, as with other clusters of imperfect models, we are likely to find that 'truth is the intersection of independent lies'[52].

Are the predictions of the geometric models confirmed?

Once the effects of geometry are removed, we can look afresh at environmental and historical influences on richness gradients. The surprise will be if the mid-domain effect turns out, after more than a hundred years of biological and historical hypotheses, to be the principal factor determining the general shape of empirical richness curves along gradients. To date, four major studies have assessed this heretical conjecture.

In their study of the distribution of bats and marsupials throughout the continental New World, Willig and Lyons[13] found that, when latitudinal distributional limits were used to approximate geographic limits for these groups as a whole, a geometric null model (Box 2) can explain 69–94% of variation in species richness patterns over the entire transect (Fig. 2). Richness for marsupials reaches its peak well south of the equator (at about 20°S), out of phase with climatic gradients, thus weakening explanations based on climate or energy.

In an analysis of the distribution of nearly 1200 species of insects and vertebrates, including 637 species endemic to the Madagascan rainforest (a biome encompassing about 13 degrees of latitude and 2100 m of elevation entirely south of the equator), Lees et al.[15] identified geometry as the most important cause of species richness gradients. A geometric null model explained far more of the variation (85% for latitude alone, 75% for latitude and longitude as orthogonal dimensions) than either area or energy (Fig. 3; Boxes 3 and 5). Latitudinally and longitudinally, species richness peaked at approximately the (mid-domain) position and the level expected from the model, given the location of biome boundaries, the empirical species range size distributions and the size of the regional species pool. However, for at least one large adaptive radiation examined[15,26], richness peaked somewhat below the middle of the elevational domain (as is common for elevational richness gradients[23]), suggesting a significant modifying influence of other factors.

In a comprehensive study of the elevational distribution of 2800 species of birds in all tropical biomes of South America (including both western and eastern slopes of the Andes), Rahbek[16] found that, once effects of area are factored out, a mid-elevation peak in species richness emerges – as predicted by geometric models, although at an elevation below the true elevational midpoint. He concluded that the mid-elevation peak is best explained by boundary constraints

(the ocean and the mountaintops), with other factors affecting the details of the gradient.

In an analysis of bathymetric richness gradients for northwest Atlantic gastropods and polychaetes, Pineda and Caswell[14] compared the parabolic richness gradients for these groups with patterns formed by randomizing the placement of empirical depth ranges. As expected, the null model also produced mid-domain richness peaks, but, for both groups, model peaks and empirical peaks were only partially matched in location, magnitude and curvature. They concluded that ' … while geometric constraints can contribute to parabolic patterns, [the] observed patterns … result from a non-random distribution of species along the depth gradient'.

In summary, work completed so far indicates a strong influence of the mid-domain effect in shaping geographic patterns of richness, when evaluated against competing biological and climatic hypotheses. The components of these patterns that cannot be predicted by geometric null models (e.g. off-centre elevational or bathymetric richness peaks or large residuals for individual sampling sites) stand out as appropriate targets of research for non-geometric explanations.

Stochastic versus deterministic perspectives

Although comparison with an appropriately constructed and parameterized geometric null model is necessary to detect the probable influence of the mid-domain effect, the demonstration of such influence neither assumes nor proves that species' ranges, or the boundaries that constrain them, are individually random in shape and in placement, with respect to ecological, evolutionary and historical causes. Of course, they are not, but the seeming paradox is a familiar one. No biologist would consider it disturbingly paradoxical that genes and environment largely determine the individual heights of a sample of 1000 adult women, whereas the distribution of their heights neatly fits a normal curve based on mean and variance in height. Analogously, the mid-domain effect is a macroecological outcome of geometric constraints that, for large numbers of taxa with their own history and adaptations, shape richness patterns along geographic gradients. These constraints arise from boundaries (both geographic limits and biological thresholds) and from an emergent statistical property of taxonomically defined biotas: their range size and midpoint distributions.

How, then, are we to view the real world relevance of a geometric null model? There seem to be two, non-exclusive approaches to interpreting empirical species richness patterns. On the one hand, we can assume that range sizes and range placements are governed by a strong element of chance. On the other hand, we could view a good fit between null models and observed species richness patterns from a deterministic perspective. Thus, ranges largely determined by the diverse adaptations and the histories of species in a regional assemblage might nonetheless fit a geometric null model, rather than yielding an emergent richness response to an environmental gradient. Lyons and Willig[19] express this view: 'Within a larger taxon such as bats or marsupials, no single factor may attain hegemony in limiting the distribution of constituent species, and as a consequence, range boundaries may have a geographic distribution that is quite similar to those produced by chance, even though different deterministic factors account for the limitations of each species.'

A specific way to reconcile the mid-domain effect with determinism is to view range overlap from a phylogenetic perspective at the species level or above. Sister populations that have diverged allopatrically or parapatrically might emerge over evolutionary time with gene frequency distributions tuned to different adaptive peaks along a cline. If speciation reaches completion, their ranges, given the opportunity, should expand or shift independently once freed from the evolutionary yoke of gene flow from source populations at the centre of the ancestral species' range[29]. Eventually, the two ranges might overlap, thus enriching a local biota. Averaged over many such cladistic events, the most probable area of overlap will be at mid-domain. Indeed, if each of the two (continuous) ranges expands to at least half the available domain, both must occur over mid-domain regions, the essence of the mid-domain effect. Such wide-ranging species tend to mask any environmental influence on local species richness[14,15]. However, in the case of two species whose ranges each span at most half the domain (narrow-ranging species), the contribution to richness at mid-domain will average less than two. The probability of two narrow-ranging species both occurring at mid-domain therefore decreases from one towards zero as the range size becomes smaller[15] (Boxes 2 and 3). Thus, the geometric theory of species richness generates a specific and highly testable prediction: that wide-ranging species or higher taxa within a

regional assemblage are considerably more likely to show patterns in accordance with geometric theory than narrow-ranging taxa[14,15,26] (Fig 3a). Geographic patterns of species richness in narrow-ranging taxa, less constrained by geometry, are more likely to reflect environmental and historical factors. Therefore, the most discerning way to test for geometric effects is to categorize data by range size class[14,15,26].

Prospects

Incorporating the geometry of ranges and of richness into local, regional and global perspectives on biodiversity promises far-reaching consequences. Geometric null models are capable of precisely predicting the expected shape and local magnitude of the interaction between geographic domains and species ranges for classes of different range size. Thus, by considering deviations from null model expectations, the prospects are good for disentangling biological, climatic and historical factors that affect species richness at different spatial and temporal scales (Box 5). The mid-domain effect emerges as a compellingly parsimonious foundation for a general theory of patterns of species richness along different gradients at a range of scales.

In effect, biogeographers and ecologists have simply had the wrong null model at the back of their minds for the past 150 years, by assuming that, were there no climatic, physical or biological gradients, species richness would be the same at all latitudes, elevations and depths. The mid-domain effect shows that mid-domain richness peaks are to be expected in the absence of such gradients. Departure from the expected richness peak, under an appropriate null model, but not the peak itself, requires biological or historical explanation at geographic scales.

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