Rapoport's rule, species tolerances, and the latitudinal diversity gradient: geometric considerations

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Abstract. The most pervasive species-richness pattern, the latitudinal gradient of diversity, has been related to Rapoport's rule, i.e., decreasing latitudinal extent of species' ranges toward the equator. According to this theory, species can have narrower tolerances in more stable climates, leading to smaller ranges and allowing coexistence of more species. We show, using a simple geometric model, that the postulated decrease of species' potential range sizes toward the tropics would itself lead to a latitudinal gradient opposite to that observed. In contrast, an increase in extent of potential ranges toward the tropics would lead to the observed diversity gradient. Moreover, in the presence of geographic barriers constraining actual species' ranges, Rapoport's rule emerges if the latitudinal trend in extents of potential ranges (as defined by climatic tolerance) is opposite to that postulated or if variability in potential range extents decreases toward the poles. A strong implicit latitudinal diversity gradient (i.e., higher concentration of midpoints of species' potential ranges in the tropics), however, produces both observed macroecological patterns without the contribution of any latitudinal trends in species climatic tolerances or in potential range sizes. Our model underscores the necessity of discriminating theoretical processes and principles from the patterns we observe, and it is well supported by data on global distribution of species' range sizes.

Key words: biodiversity; biogeography; equatorial effect; implicit latitudinal gradient; macroecology; mid-domain effect; physiological tolerance; potential range; Rapoport's rule; Stevens's principle.

INTRODUCTION

Dozens of hypotheses attempt to explain increasing species richness toward the tropics observed in a majority of taxa (e.g., Willig et al. 2003, Hillebrand 2004). Stevens (1989) associated this pattern with Rapoport's rule, i.e., the decrease in mean latitudinal extent of species' ranges toward the tropics (Rapoport 1975). Stevens (1989) hypothesized that this pattern is derived from the requirement that organisms living at high latitudes have broader environmental tolerances due to larger seasonal fluctuations. Tropical species, conversely, may have more specialized habitat requirements and narrower tolerances, permitting coexistence of more species. Stevens also postulated that dispersal of narrowly distributed habitat specialists into less favorable areas may enhance local richness in the tropics through mass effects (Shmida and Wilson 1985) or rescue effects (Brown and Kodric-Brown 1977) on sink populations of species with narrow tolerances.

Although Stevens himself stated that the latitudinal diversity gradient is caused by Rapoport's rule, it is

apparent that, according to his hypothesis, it is rather the principle of changing environmental tolerance of species with latitude, and consequently the latitudinal trend of individual's and species' potential to survive in various latitudes, that leads to both the diversity gradient and Rapoport's rule. It is therefore essential to distinguish *Rapoport's rule*, as the observed poleward increase in the mean latitudinal extent of species ranges, from what we will call *Stevens's underlying principle*, i.e., the poleward increase of mean *potential* extents of latitudes inhabitable by a species.

Attempts to empirically evaluate Rapoport's rule brought equivocal results (Rohde et al. 1993, Gaston et al. 1998, Kerr 1999, Taylor and Gaines 1999, Cardillo 2002, Smith and Gaines 2003, Fortes and Absalão 2004, Ruggiero and Kitzberger 2004, Arita et al. 2005, Morin and Chuine 2006, Ruggiero and Werenkraut 2007). Some studies dealt with possible biases in the data (Blackburn and Gaston 1996), demonstrating that the pattern is confined only to particular latitudes (Rohde 1996) and is not symmetric about the equator (Gaston and Chown 1999*a*, Orme et al. 2006). Only a few studies have compared the observed patterns with null models, and not all were explicit about the assumed underlying mechanisms (Colwell and Hurtt 1994, Lyons and Willig
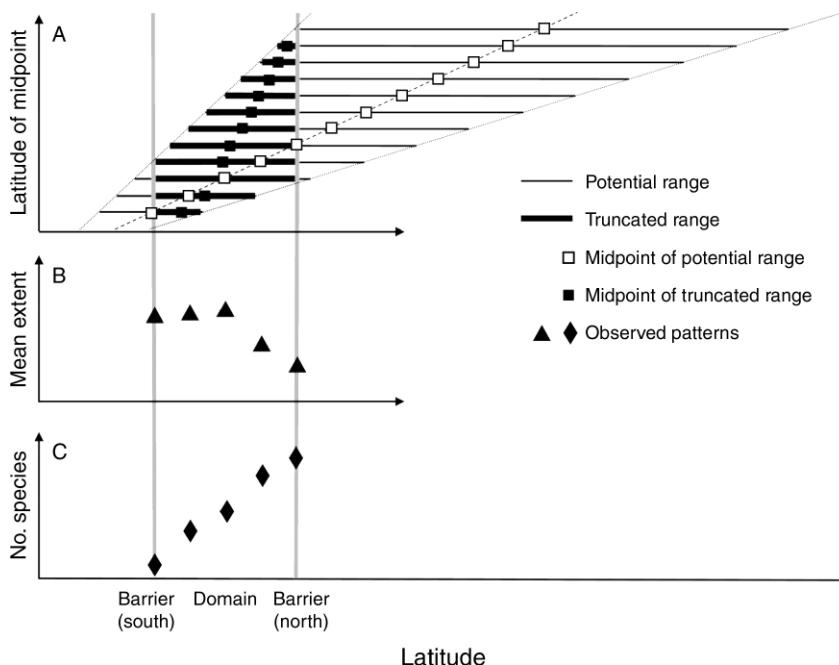
FIG. 1. A case example of the effect of truncating potential ranges. (A) Here, extents of potential ranges increase with latitude. All truncated ranges lie within the domain with midpoints closer to the center of the domain than before truncation. (B) The observed mean extent–latitude relationship (triangles) changes its shape and slope. (C) The species richness–latitude relationship (diamonds), however, remains unchanged.

1997, Taylor and Gaines 1999, Grytnes and Vetaas 2002, Arita 2005, Ribas and Schoereder 2006). Only Taylor and Gaines (1999) and Gryntes and Vetaas (2002) considered possible trends in potential range sizes as factors affecting underlying mechanisms. Part of the problems with exploring Rapoport's rule arose from differences in how the relationship between mean extent and latitude was measured (Rohde et al. 1993, Gaston et al. 1998, Gaston and Blackburn 1999; but see Rohde 1999). Two methods are usually employed. Stevens (1989) used the latitudinal extent of all the ranges overlapping a focal latitude for the calculation of mean extent, and correlated it with focal latitude. This method was called *Stevens's method* (Gaston et al. 1998) and was criticized for autocorrelation problems. To circumvent this, only those ranges whose midpoints fell within a given latitudinal band were used to calculate mean extent (Rohde et al. 1993). This method was called the *midpoint method*.

Another major problem with Rapoport's rule concerns the relationships between the latitudinal diversity gradient, latitudinal trends in potential range extents, and observed patterns (Kolasa et al. 1998). Observed ranges may represent only parts of potential ranges, because realized ranges can be truncated by barriers (coastlines, mountain ridges) unrelated to latitude-dependent species' environmental tolerances (Araújo and Guisan 2006, Sandel and McKone 2006). This potentially affects all relationships between latitudinal position and latitudinal extent of observed ranges (Fig.

1). While some of these issues have been addressed in more detailed studies (Colwell and Hurtt 1994, Blackburn and Gaston 1996, Rohde 1996, Lyons and Willig 1997, Gaston and Chown 1999a, Taylor and Gaines 1999, Ribas and Schoereder 2006), each of them deals with only a particular topic. A general theory which would separate geometrical artifictions (false patterns with geometrical drivers; see Palmer et al. 2008) from biologically relevant effects is thus crucially needed. Such a theory should encompass all the possible relationships between latitudinal trends in potential range sizes and observed patterns which are necessarily distorted by the latitudinal trends as well as latitude-independent barriers.

Here we develop a theory based on the geometry of all possible combinations of latitudinal trends in potential range extent, latitudinal diversity gradient, and barriers truncating realized ranges. The aim of the theory is to discriminate between geometric and biological components of the observed patterns. We show that the appropriate geometric considerations reveal surprising relationships: First, Stevens's underlying principle itself can generate a latitudinal diversity gradient which is opposite to that usually observed, whereas the usual latitudinal diversity gradient (i.e., poleward decrease of diversity) could potentially be generated by the opposite of Stevens's underlying principle. Second, Stevens's underlying principle leads to an opposite Rapoport's rule, whereas Rapoport's rule is generated by opposite Stevens's underlying principle in the presence of barriers

truncating potential ranges. Third, in the presence of a strong implicit latitudinal diversity gradient, Rapoport's rule would be generated even without the poleward increase in potential ranges. Fourth, the midpoint method of evaluating latitudinal trends in range size is incapable of revealing Stevens's underlying principle if ranges are truncated by barriers.

THE THEORY

Concepts, assumptions, and terminology

We restrict our exercise to one dimension, corresponding to the distribution of species along a single meridian (Fig. 2). The extent of range along a single meridian does not necessarily correspond with the interval between the northernmost and southernmost boundaries of a two-dimensional range. By modeling along a meridian we avoid the issues related to summing across many climatically unique latitudinal bands (Kaufman and Willig 1998). The word *range* hereafter refers to the one-dimensional uninterrupted range. By *species richness* we will mean the number of ranges overlapping a point of latitude.

Central to the theory is a difference between species' potential, truncated, and realized ranges (Fig. 2), corresponding with Hutchinson's (1959) distinction between fundamental and realized niches (see Soberon 2007). Range boundaries are in many cases determined by dispersal *barriers*, and overcoming such barriers leads to broadening of species range, as known from species invasions (e.g., great American exchange; Brown and Lomolino 1998). *Potential range* is a latitudinal extent along the meridian between the northernmost and southernmost points with suitable environmental conditions that would be inhabited by species, had there been no barriers. *Realized species' range* is the latitudinal extent between the northernmost and southernmost points of species actual occurrence. It may be affected by dispersal abilities and particular arrangement of barriers (Fig. 2). Range affected (truncated) by at least one barrier is *truncated range*. Potential range that is not affected by any dispersal barrier is equivalent to realized range. Hence, not all realized ranges are necessarily truncated.

The realized range is always smaller than or equal to the potential range, and truncated range is always smaller than potential range. We call the latitudinal limits of a potential range *potential limits* and the distance between them *potential extent*. Latitudinal distance between two barriers or between a barrier and potential limit will be called *truncated extent*. The space between any two barriers, each affecting at least one range, will be called a *domain*.

We will assume, in accord with Stevens's approach, that latitudinal extent of potential ranges changes systematically with latitude (possibly due to changing environmental tolerance of species). On the other hand, since the barriers which truncate a given range are considered to act independently from each other, range
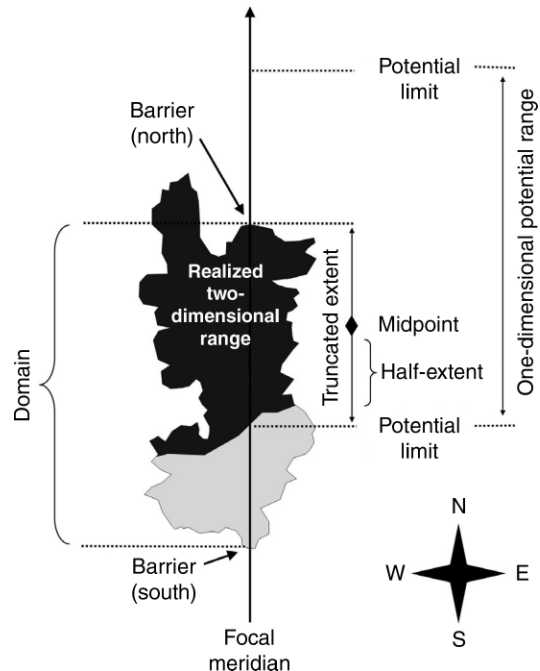

FIG. 2. Illustration of the most important terms. The figure can be viewed as a continent surrounded by an ocean. Truncated extent is meridian specific, for it refers to the part of the realized range (black) along a focal meridian. Note that the latitude of a potential limit may vary between meridians, because each meridian is climatically unique.

truncation itself should not cause latitudinal trends in range extents. The distinction between potential and realized ranges is thus a necessary feature of the model—we need to separate latitude-dependent limits (i.e., those on which some general principle, e.g., Stevens's underlying principle, applies) from those that are latitude independent (i.e., on which no general principle can apply). Whereas the potential limits may occur everywhere and can be attributed to latitude, latitude-independent limits are set only by existing geographical barriers.

Each latitudinal gradient is by definition bounded by the equator and the pole. Poles represent barriers rather than potential limits, because even if a species' climatic tolerance potentially allowed persistence in harsher conditions than at the pole, it cannot spread further behind the pole. We will thus take the poles as universal barriers for all species. The equator is rather peculiar: all potential ranges which overlap the equator must shift their midpoints toward the equator. In an ideal case of a virtual world which is climatically symmetric about its equator, the potential ranges overlapping the equator spread symmetrically about it. This enlarges the potential extent in the tropics and elevates potential species richness there, regardless of the latitudinal gradient in potential extents (i.e., Stevens's or opposite Stevens's underlying principle) and regardless of only rough symmetry of climatic patterns (France 1998; see
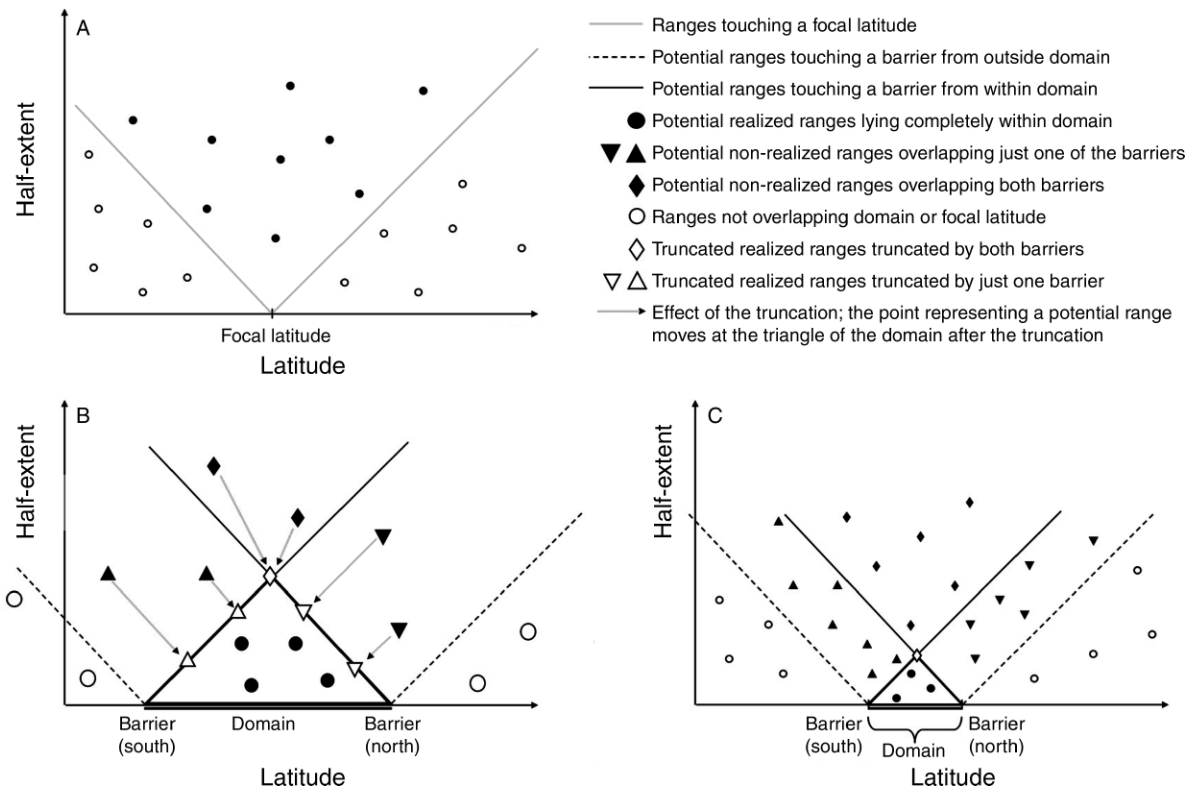
FIG. 3. The bivariate space defined by latitude and half-extent of modeled objects. (A) Ranges that do not overlap a focal latitude (and thus do not contribute to its species richness) are represented by points lying outside the area between the two dotted identity lines that intersect the focal latitude at the horizontal axis; ranges that overlap the latitude lie between these two lines. (B) The points representing ranges truncated by only one barrier shift parallel to identity lines down to the sides of the triangle. The points representing ranges truncated from both sides move down to the top of the triangle (the point also representing the half-extent of the domain). (C) Potential ranges can overlap the domain (completely or partially), lie completely within the domain, or lie completely outside of the domain. Each of these situations corresponds to a defined space in the biplot. The thick lines along the x-axis in panels (B) and (C) represent the domain.

Chown et al. [2004] for a review). We call this *the equatorial effect*.

The geometric model

Our model is defined in a bivariate space defined by (1) latitude (*x*-axis) and (2) half-extent (*y*-axis). We recognize three sorts of objects in the bivariate space: [*object 1*], points with half-extent >0 representing species *ranges* (their coordinates refer to latitudes of their midpoints and their half-extents, Fig. 3); [*object 2*], points at the latitude axis (half-extent = 0) representing *barriers* or *focal latitudes* (their positions at the latitude axis refer to their location along given meridian); and [*object 3*], lines representing the maximum and minimum *constraints* of half-extents of potential ranges of various classes (solid lines in Fig. 4, which can define possible latitudinal trends in half-extents of potential ranges; e.g., Stevens's underlying principle).

The three types of objects obey the following rules:

Rule 1.—All ranges contributing to species richness of any focal latitude obey the formula $|m - f| \leq r$, where *f*, *r*, and *m* are midpoint latitude, half-extent of a range, and focal latitude, respectively. They thus lie in the space between two lines with slopes +1 and −1 originating from the horizontal axis at the focal latitude (dashed lines in Fig. 3A).

Rule 2.—All ranges with edges exactly at the focal latitude lie on either of the lines. These lines are crucial for further reasoning, and are hereafter called *identity lines*.

Rule 3.—Any range which is truncated by only one barrier lies on the same identity line as its corresponding potential range. The reason is that if a rage is truncated, the shift of its midpoint and the reduction of its half-extent are equal (arrows in Fig. 3B).

Rule 4.—All ranges truncated by one barrier lie exactly at the sides of the triangle (analogous to the triangle in Colwell and Hurtt [1994]) delimited by two barriers and the point representing the whole domain, but never at its very top.

Rule 5.—Only ranges truncated by both barriers of a domain occur at the apex of the triangle. (Rules 4 and 5 follow from the rules 1 and 3.)

Rule 6.—All realized ranges in a domain lie within the triangle (including its sides).

Rule 7.—All potential ranges lie between two constraints that delimit the range of potential extents for each latitude (object 3; for example, full lines in Fig. 4; however, so far we do not assume anything about their exact positions).

Rule 8.—The bivariate space is divided into six uninterrupted areas, each containing particular sort of potential ranges: (1) two areas that do not overlap the domain of concern, (2) those truncated by only the northern barrier, (3) those truncated by only the southern barrier, (4) those truncated by both barriers, and (5) those not truncated at all (Fig. 3C).

Rule 9.—Vertical distance between ranges shows their difference in terms of size; horizontal distance between ranges shows differences in location along the latitudinal gradient. If there is no latitudinal bias in both distances, we say that there is no *implicit latitudinal gradient* (in potential range similarity). Closer spacing of potential ranges at low latitudes produces our *implicit latitudinal gradient*. The reverse trend produces our *opposite implicit latitudinal gradient*.

The model captures the crucial relationships between potential and realized ranges. It leads to following consequences:

Consequence 1.—*Stevens's underlying principle itself produces an opposite latitudinal gradient in species richness to that typically observed.*

Stevens's underlying principle says that mean extent (and so half-extent also) of potential ranges increases with latitude of their midpoints. In our model this can be produced by two increasing constraint lines (Fig. 4; rule 7). The area bounded by two parallel increasing constraints (Fig. 4A solid lines) and two identity lines (Fig. 4A dashed lines; rule 1) is larger at higher focal latitudes then at low ones (Fig. 4A). The same applies if the increasing constraints diverge with latitude. Hence, with no implicit latitudinal gradient, number of ranges contributing to species richness at higher latitudes is higher than number of ranges at low latitudes (rule 9). Apparently, decreasing species richness with latitude can only be observed if (1) there are strongly converging constraints (Fig. 4B), (2) the constraints are decreasing (reversing Stevens's underlying principle), or (3) there is a strong implicit latitudinal gradient (Fig. 4C).

Consequence 2.—*Removing truncated ranges from the analysis does not reveal any latitudinal trend in extents of potential ranges and artificially produces the mid-domain effect.*

By removing all truncated ranges, one removes all points lying on the sides of the triangle (Fig. 3B; rules 4 and 5). Because the triangle is taller in the middle of the domain, the midpoints of the largest non-truncated ranges will be concentrated in the middle of the domain in the case of no implicit latitudinal gradient. This creates a peak of both mean range extent and species richness in the center of the domain (see figures for
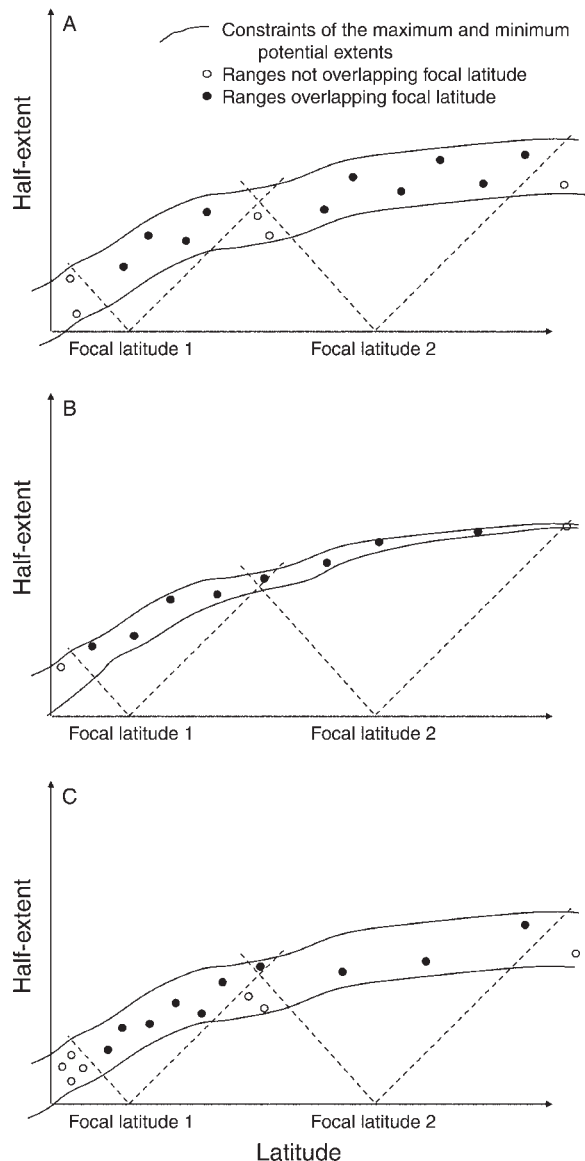

FIG. 4. Relationship between Stevens's underlying principle (represented by two increasing constraints of potential half-extents), an implicit latitudinal gradient, and the observed latitudinal gradient in species richness. (A) If the distribution of midpoints in the plot is regular, then the number of species at each latitude is given by the size of the area bounded by the constraints and the dashed identity lines. If the constraints are parallel, the number of species increases with latitude. The typical decreasing diversity–latitude relationship can be caused (B) by decreasing interspecific variance in latitudinal extent (converging constraints) and/or (C) by an implicit latitudinal gradient (higher density of points in low latitudes).

models 2–4 in Colwell and Hurtt [1994]). The more ranges have half-extents of about half height of the triangle, the stronger is the effect. This peak of species richness is called mid-domain effect (Colwell and Hurtt 1994, Hawkins and Diniz-Filho 2002, Sandel and McKone 2006). An implicit latitudinal gradient or

opposite implicit latitudinal gradient shifts the peak in species richness toward one of the barriers.

Consequence 3.—If ranges are truncated, the relationship between mean half-extent and latitude of midpoint says nothing about Stevens's underlying principle when using the midpoint method.

The midpoint method calculates the mean extent using species whose midpoints fall within a narrow latitudinal band. Realized ranges are either truncated, occurring at the sides of the domain triangle (Fig. 3B; rules 4 and 5), or not truncated, located inside the triangle (rule 6). Hence, any empirical evaluation of the relationship between the latitude of midpoints and half-extents is determined by the triangle and strongly affected by the proportion of truncated and non-truncated ranges at each latitudinal band. This proportion does not reflect changes in potential extents but changes in their interspecific variation with latitude (i.e., changes in the length of the identity line between upper and lower constraints in the case of no implicit latitudinal gradient; rules 3, 7, and 9). This proportion can also be affected by an implicit latitudinal gradient. Clearly, any latitudinal trend in potential extents (Stevens's underlying principle) is masked by the truncation. Removing truncated ranges (i.e., points along the sides of the triangle) *cannot* help (1) because of Consequence 2 and (2) because we never know whether the ranges inside the triangle of the focal domain are really non-truncated, i.e., whether they are not subjects of truncation by some other barrier.

Consequence 4.—If ranges are truncated, the Stevens's method produces hump-shaped extent–latitude relationships.

Stevens's method calculates the mean extent using all species whose ranges overlap focal latitude. Species richness at the focal latitude is given by the number of points between two identity lines (Fig. 3A; rules 1 and 9). Points representing truncated ranges lie at the sides of the triangle with the peak in the middle of the domain (Fig. 3B; rules 4 and 5). If we move from any of the barriers toward the center of the domain, the set of species we detect is necessarily enriched with species with large truncated ranges and impoverished of species with small truncated ranges. This is because species with large truncated ranges can only have midpoints close to the center of the domain, while species with small truncated ranges can only have midpoints close to the barriers. Similarly, midpoints of large non-truncated ranges can lie only in the center of the domain, whereas small ranges can lie almost anywhere if there is no implicit latitudinal gradient. Observed mean extent thus increases as one moves from the edge of the domain toward its center. Stevens's underlying principle cannot change this result. The implicit latitudinal gradient can only shift the summit of the hill-shaped curve north or south. Only very special nonrandom distributions of non-truncated realized ranges can produce more summits on the hump-shaped pattern, a case we consider unlikely.

Consequence 5.—If ranges are truncated, Stevens's underlying principle produces opposite Rapoport's rule, and opposite Stevens's underlying principle produces Rapoport's rule.

Let us show this effect in mean extents calculated for truncated ranges (i.e., those touching the barriers; the non-truncated ranges thus will not affect our evidence). In the case of no implicit latitudinal gradient and two increasing constraints (Stevens's underlying principle), points representing potential ranges that touch the southern barrier after truncation lie in the space delimited by identity lines α and β (Fig. 5; rules 1 and 2). Similar reasoning applies for the northern barrier (identity lines γ and δ). Mean latitudinal extents observed exactly at the barriers depend solely on the frequency distribution of midpoints along the edges of the triangle of the domain. If there is a majority of small truncated ranges, mean extent is small at the barrier, and vice versa. As can be seen in Fig. 5, the proportion between the number of large and small truncated ranges is $(L + C)/S$ (L and S are for large and small ranges, respectively; C indicates the number of ranges truncated by both barriers). If the increasing constraints are parallel (Fig. 5A), the proportion $(L_n + C)/S_n$ for the northern barrier is always smaller than $(L_s + C)/S_s$ for the southern barrier. This effect produces a left–right asymmetric hump-shaped curve (Fig. 1B; consequence 4) with decreasing regression line: the opposite of Rapoport's rule. If the constraints are diverging with latitude, the result does not change. The only exceptions represent the cases of either (1) strongly converging constraints at high latitudes and/or (2) a strong implicit latitudinal gradient (Fig. 5B, C). In such cases, we can observe Rapoport's rule even in the presence of Stevens's underlying principle. Apparently, the more converging the constraints are, the smaller is S_n and the larger is S_s, leading to closer correspondence between Rapoport's rule and Stevens's underlying principle. In addition, very strong convergence of the constraints at some latitudes can compensate for the divergence of these constraints elsewhere (Fig. 5D). In this case we can observe Rapoport's rule in the presence of Stevens's underlying principle, even though there are latitudes with diverging constraints. Note that this case is sensitive to the position of the constraints relative to the domain; the constraints have to converge below and diverge above the midpoint of the domain, and thus some biological mechanisms adjusting species tolerances to the domain are needed.

The situation is more complicated in the case where many potential ranges lie completely inside the domain. This can happen when one (or both) constraints intersect the triangle of the domain. As we will show using numerical simulations, the effect of truncation prevails even in this case.

Consequence 6.—A strong implicit latitudinal gradient necessarily affects mean latitudinal extent, thus producing Rapoport's rule.
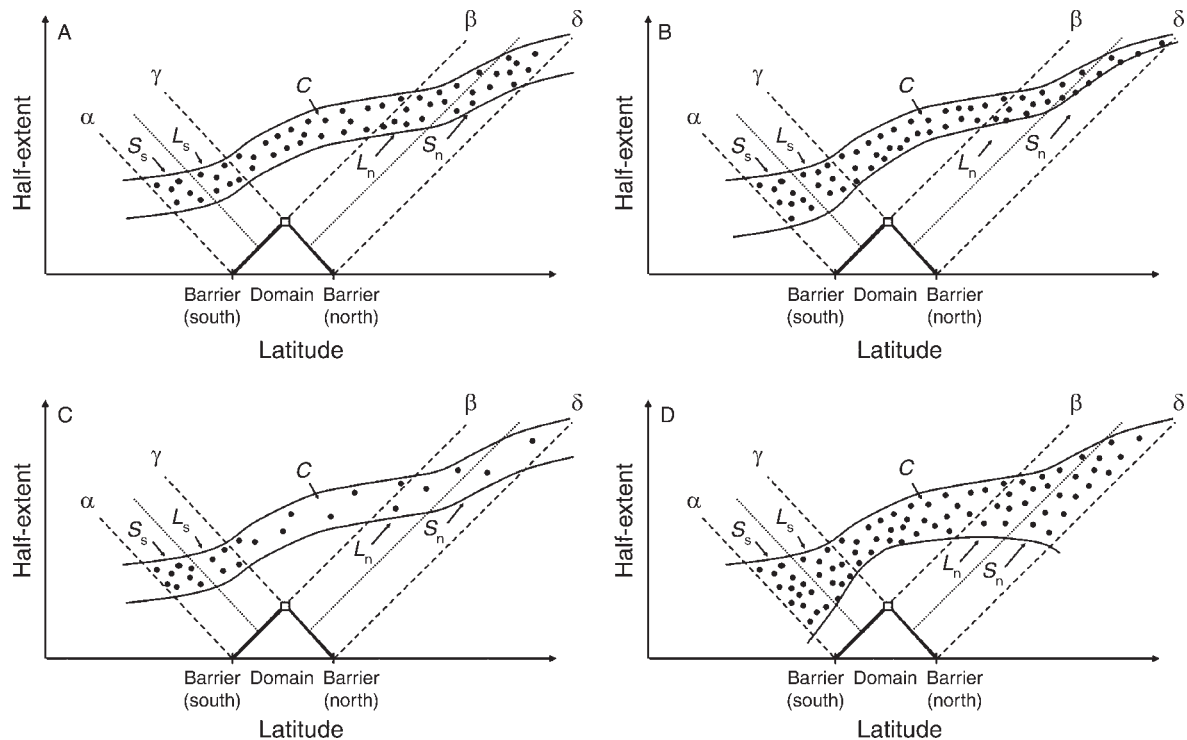
FIG. 5. The evidence that Stevens's underlying principle produces a reversed Rapoport's rule. Stevens's underlying principle is represented by the two increasing constraints on potential ranges (solid lines). Subscripts (s and n) indicate areas in the biplot where potential ranges overlap the southern (s) and northern (n) barrier. Points representing all truncated ranges lie on the sides of the triangle of the domain (see Fig. 3B). (A) With no implicit latitudinal gradient, the ratios between large (L) and small (S) truncated ranges, where C is the number of ranges truncated by both barriers, $(L + C)/S$, are 26/6 and 31/11 for the southern barrier and northern barrier, respectively. The smaller value at the northern bound corresponds to an opposite Rapoport's rule, so the Stevens's underlying principle does not coincide with Rapoport's rule in this case. (B) If the constraints converge with latitude, the areas between them are relatively larger for smaller truncated ranges in southern latitudes and for larger truncated ranges in northern latitudes (here $[L_s + C]/S_s = 32/9 < 35/8 = [L_n + C]/S_n$). This leads to increased mean observed extent with latitude. (C) Rapoport's rule also emerges when a strong implicit latitudinal gradient exists. (D) If interspecific variability increases for some ranges of latitude but is compensated by a strong decrease elsewhere, Rapoport's rule can coincide with Stevens's underlying principle, but this requires special arrangements of the domain and the constraints. None of the results is sensitive to exact placement of identity lines dividing S_s from L_s and S_n from L_n; we placed identity lines in the middle of the sides of the triangle for visual clarity.

Apparently, a strong implicit latitudinal gradient affects the proportions of ranges corresponding to areas S_s, L_s, S_n, and L_n (Fig. 5; consequence 5). It can be seen from Fig. 5D that the implicit latitudinal gradient enlarges the proportion of species with both small truncated ranges at the left side of the triangle (S_s) and large truncated ranges at the right side of the triangle (L_n). This produces Rapoport's rule regardless of the direction of Stevens's underlying principle. However, this only happens if the implicit latitudinal gradient is strong enough to violate the following inequality:

$$\frac{\text{no. ranges in } L_s + C}{\text{no. ranges in } S_s} > \frac{\text{no. ranges in } L_n + C}{\text{no. of ranges in } S_n}. \quad (1)$$

Consequence 7.—The equatorial effect produces an implicit latitudinal gradient.

This occurs because the ranges that would be truncated by the equator actually exceed it and spread into the opposite hemisphere, moving their midpoints toward the equator. The tendency toward a stronger implicit latitudinal gradient (and thus all its consequences) emerges even if extents are not allowed to be fully symmetrical about equator.

Consequence 8.—Spherical shape of the globe might invert the implicit latitudinal gradient.

If (1) east–west extents (measured as a length along a parallel) of two-dimensional ranges are independent of latitude or (2) if they increase with latitude, then more ranges overlap the focal meridian at high latitudes, increasing the density of points representing ranges in those latitudes and potentially leading to an inverted implicit latitudinal gradient. Strength of implicit latitudinal gradient is thus an independent variable of the model, which is affected not only by evolution and ecology of species in various latitudes but also by the shape of the globe and a latitudinal gradient in the east–west extents of species ranges.

TABLE 1. Definitions of the terms used in the text.

Term	Definition
Potential limits	Two points at a meridian that define the northernmost and southernmost latitudes at which the species can potentially live and reproduce, given by its environmental tolerance and environmental conditions along the meridian. They are species specific.
Potential range	Latitudinal range between potential limits. Stevens's principle suggests that it varies systematically with latitude because of changes in species' environmental tolerance with latitude.
Barrier	Two points at a meridian that define the northernmost and southernmost impenetrable barriers. In reality, barriers would be species specific and determined by species' dispersal abilities. However, we assume (1) that there are barriers shared by the focal species group and (2) that their latitudinal positions are mutually independent.
Realized range	Latitudinal range between the northernmost and the southernmost point of species' actual occurrence. The range is defined by potential limits and/or barriers (realized range is not necessarily truncated).
Truncated range	A realized range that was truncated by at least one barrier. Ranges whose potential limit would accidentally coincide with a barrier (which is unlikely) were taken as truncated.
Constraints	Two curves in the bivariate half-extent–latitude space (Figs. 4 and 5) that constrain maximum and minimum potential half-extents of species' ranges at each latitude.
Implicit latitudinal gradient	Decrease of the density of range midpoints in the bivariate half-extent–latitude space. The absence of implicit latitudinal gradient implies that midpoints of potential ranges are regularly or randomly distributed between the two constraints.
Identity line	A line with slope of +1 or −1 originating from the horizontal axis at a focal latitude. Any range along an identity line has identical half-extent and distance between their midpoint and the focal latitude.
Triangle of the domain	A triangle formed by two barriers (points at latitude axis) and a point representing the domain. Two sides of the triangle lie on identity lines attaining the barriers.
Equatorial effect	A consequence of the fact that environmental conditions have an extreme (either maximum or minimum) at the equator. This causes potential ranges overlapping the equator to spread more or less symmetrically about it, enlarging potential ranges near the equator, and affecting the implicit latitudinal gradient by increasing density of range midpoints there.

Numerical simulations

To support our geometric reasoning, we performed numerical simulations of 500 one-dimensional worlds. There was one domain in each world and 50 000 potential ranges overlapping the domain. The simulated worlds exhibited either Stevens's underlying principle or its opposite form. In each world we recorded species richness and mean latitudinal extents (Stevens's method) at 100 latitudes randomly drawn from the latitudinal extent of the domain. (Since all comparisons were proportional, the latitudinal extent of the domain was not relevant.) The constraints of minimum and maximum potential extents (Table 1; solid lines in Fig. 4) were chosen randomly (intercepts and slopes were distributed uniformly) for each simulated world, using only the following rules: (1) maximum and minimum constraints are approximated by lines with slopes between −1 and 1; (2) maximum constraints lie above the triangle of the domain (i.e., potential ranges that are truncated by both barriers of the domain do exist); (3) the intersection of the constraints is either outside of the area of ranges overlapping the domain or the constraints are parallel (i.e., the variance of latitudinal extents changes monotonically with latitude or is latitude independent).

Four sets of simulations were carried out: (1) no implicit latitudinal gradient and no equatorial effect, (2) an implicit latitudinal gradient strong enough to produce the latitudinal gradient in species richness ($\sigma_{(\lambda)} = e^{-C\lambda}$, where σ is a latitudinal density of midpoints

at the latitude of λ and $C = 0.05$) and no equatorial effect, (3) an equatorial effect and no implicit latitudinal gradient, and (4) both effects. Then we calculated the slopes of regression lines for both the relationship between latitude and species richness and the half-extent–latitude relationship measured by Stevens's method. Negative slopes of the diversity–latitude relationship indicate the generally observed latitudinal gradient in species richness, and positive slopes of the half-extent–latitude relationship indicate Rapoport's rule. The applicability of Stevens's and/or opposite Stevens's underlying principle were assessed by averaging the slopes of the minimum and maximum constraints.

All geometric consequences listed here were supported by the simulations (Fig. 6). The results of simulations with equatorial effect are not reported here as they were qualitatively equivalent to those with implicit latitudinal gradient. The opposite Stevens's underlying principle (negative mean slopes of the constraints) produces the typically observed latitudinal gradient in species richness (negative slopes) regardless of the implicit latitudinal gradient (Fig. 6A, B). If there is no implicit latitudinal gradient (Fig. 6A), there are some points conforming to both Stevens's underlying principle and to the typically observed gradient in species richness. These represent simulations with strongly converging constraints (i.e., poleward decrease in the variance of potential extents; see Fig. 4B). If there is no implicit latitudinal gradient, Stevens's underlying principle produces the opposite
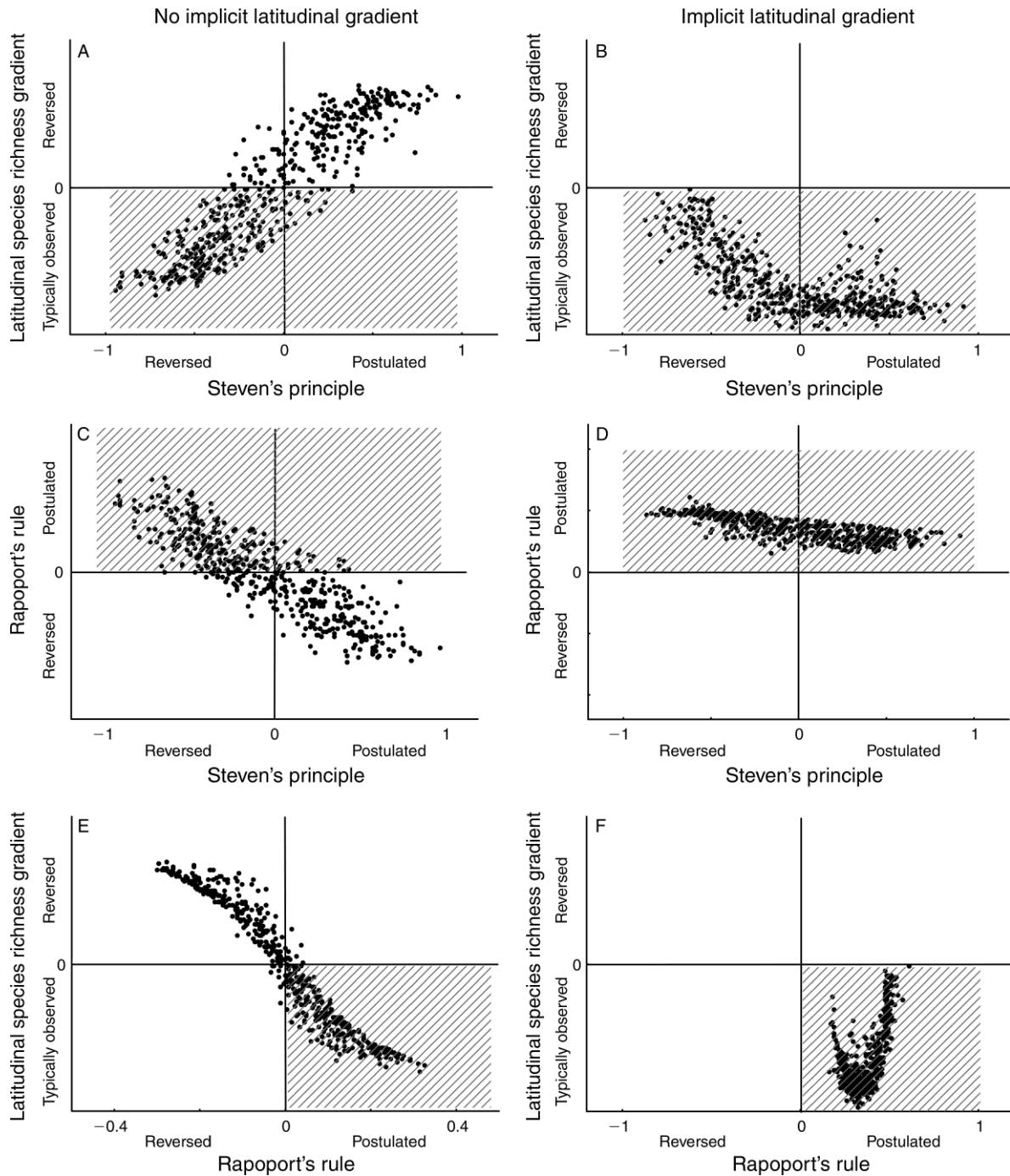
Fɪɢ. 6. Outputs of 500 simulations (each with 50 000 ranges) varying in applicability of Stevens's underlying principle. Each point shows the slopes of two regression lines derived from virtual observations of ranges and species richness at 100 randomly chosen latitudes. The typically observed regions of slopes are highlighted by hatching. Columns contrast simulations (A, C, E) with and (B, D, F) without an implicit latitudinal gradient. Panels (A) and (B) show the dependence of latitudinal diversity gradient on Stevens's underlying principle. Values on the horizontal axes are slopes of regression lines between mean half-extent and latitude (Stevens's underlying principle as postulate yields positive slopes); values on the vertical axes are for regressions of species richness on latitude (the typically observed latitudinal gradient indicated by negative values). Panels (C) and (D) show the relationship between Stevens's underlying principle and Rapoport's rule in the world with a bounded domain; values on the vertical axes are for regressions of range extent against latitude (the standard Rapoport's rule produces positive values). Panels (E) and (F) show the coincidence of the Rapoport's rule and the latitudinal gradient in species richness.

trend of Rapoport's rule, while the opposite Stevens's underlying principle produces Rapoport's rule (Fig. 6C). If there is a strong implicit latitudinal gradient, Rapoport's rule applies regardless of the direction of Stevens's underlying principle (Fig. 6D).

Regardless of implicit latitudinal gradient, Rapoport's rule coincides with the latitudinal diversity gradient, as it is generally assumed (Fig. 6E, F). There is, however, no causal link between these two patterns. A strong implicit latitudinal gradient causes this coincidence regardless of the direction of Stevens's underlying principle (compare Fig. 6D, F). If the implicit latitudinal gradient is weak or lacking, a reversed Stevens's underlying principle or a decreasing variability in potential extents with latitude (converging constraints) is required to obtain typically observed latitudinal diversity gradient (compare Fig. 6C, E).

Discussion

We have shown that in principle both the observed latitudinal diversity gradient and Rapoport's rule may be consequences of the same effect: a poleward decrease in the extent of potential ranges (caused by an unknown biological mechanism). If potential species range sizes increase toward the equator, more ranges overlap each other in the tropics, whereas the observed latitudinal extents increase from the tropics to the poles due to the effect of truncation (see Figs. 1B, 5). Rapoport's rule would then be a consequence of the opposite effect of that assumed by Stevens (1989). However, in the presence of a strong implicit latitudinal gradient (which could be caused by the mechanism postulated by Taylor and Gaines [1999] or any other process suggested as the cause of the gradient; see Willig et al. [2003], Mittelbach et al. [2007]), Rapoport's rule would apply in a bounded domain regardless of Stevens's underlying principle, and would be the simple consequence of the strong implicit latitudinal gradient. The combination of a weak implicit latitudinal gradient and Stevens's underlying principle can produce either an opposite or hump-shaped latitudinal diversity gradient.

Regardless, neither the midpoint method nor the Stevens's method provides direct information about the processes underlying the observed pattern. The midpoint method gives results strongly determined by the truncation of the domain while the Steven's method would have to assess the implicit latitudinal gradient to eliminate the effect of range truncation. In other words, Rapoport's rule is not a signal of Stevens's underlying principle, i.e., of the tendency to enlarge potential ranges toward the poles due to latitudinal trend in species climatic tolerances (for alternative evidence, see Lyons and Willig 1997). Additionally, both methods necessarily produce locally (within domain) increasing or decreasing range extents with latitude, which has been referred as the local Rapoport's rule (Blackburn and Gaston 1996, Rohde 1996, Gaston and Chown 1999b).

Our theory considers all possible combinations of latitudinal trends in potential range sizes, their truncation, and implicit latitudinal gradients, and demonstrates that different combinations may produce equivalent observed patterns. This makes it difficult to evaluate which combinations of processes are operating in nature based on published results. However, there is still room for the interpretation of the patterns observed in nature, given consideration of geometric limitations. First, if we have good reasons to assume that there is no implicit latitudinal gradient, the latitudinal trend in range extents is revealed by the asymmetry of the hump-shaped curve obtained by Stevens's method (see Fig. 1B). Second, non-truncated ranges can reveal an implicit latitudinal gradient. This is, however, complicated by the fact that several domains truncating ranges can be nested (e.g., biomes within continents) or mutually overlapping, and each potential range can be consequently truncated by different pairs of barriers. Non-truncated ranges are thus hard to detect. On the other hand, multiple domains can be detected in the half-extent–latitude biplot, where the barriers shared by several species should form apparent identity lines (slopes of 1 or −1) (see figures in Ribas and Schoereder 2006). These biplots can thus be used for detecting barriers and for revealing biogeographical units (i.e., domains) and their effect on latitudinal trends in range extents.

Most studies of latitudinal range-size variation (e.g., Rapoport 1975, Stevens 1989, Rohde et al. 1993, Gaston et al. 1998, Kerr 1999, Rohde 1999, Smith and Gaines 2003, Fortes and Absalão 2004, Morin and Chuine 2006) comprised only a particular bounded domain, which produces artifacts due to the range truncation. The most comprehensive global study comprising ranges of all land bird species (Orme et al. 2006) indicates that the most probable combination of effects is Stevens's underlying principle together with a strong implicit latitudinal gradient. Their figures (Orme et al. 2006: Fig. 3A–E) show that, moving from the north pole to the equator, median range size first increases and then (at ~50° N) decreases toward the equator; the same general pattern is repeated in the southern hemisphere, though it is much less prominent. This pattern corresponds with hump-shaped patterns produced by our simulations when potential ranges are truncated by domain boundaries. Because the data combine patterns from a number of meridians, the pattern results from the combination of several hump-shaped curves. The visible peaks are at approximately 50° N, 11° N, 17° S, and 28° S (Orme et al. 2006: Fig. 3E), corresponding with the midpoints of palearctic–nearctic (30–70° N and 20–70° N), oriental north of the equator (0–20° N), afrotropical south of the equator (0–35° S) and neotropical south of the equator (0–55° S) regions, respectively. Because the domains of the southern hemisphere are generally smaller, the mean extents are also smaller and the resulting pattern appears to be generally decreasing from north to south. As the

figure combines data from both hemispheres, the potential signal of Stevens's underlying principle is hidden. Regardless, the small extents at very low latitudes as well as presence of a small peak around the actual equator may indicate narrower species tolerances in the tropics, and consequently Stevens's underlying principle combined with a strong implicit latitudinal gradient. The combination of the reversed Stevens's underlying principle and a weak, or absent, implicit latitudinal gradient cannot, however, be rejected.

Our model of the spatial distribution of ranges and consequential patterns along the latitudinal gradient differs substantially from the model of Colwell and Hurtt (1994), which produces the mid-domain effect. The process of range assembly that generates the peak of diversity in the center of the bounded domain assumes that ranges cannot exceed the domain-bounding constraint, so that centers of large ranges have to move toward the center of the domain, causing the increase in species richness away from the boundary while at the same time maximizing mean range size at the center of the domain and lowering species turnover there due to the lower density of range edges (Koleff and Gaston 2001). No such pattern has been actually observed (Koleff and Gaston 2001). Our theory is more versatile than the model of Colwell and Hurtt (1994), which cannot incorporate the implicit latitudinal gradient nor any trend in potential ranges. Moreover, their model can be explored within the framework of our theory (consequence 2).

The results of Taylor and Gaines (1999) resonate with ours, but by considering all possible combinations we revealed that Rapoport's rule can be "rescued" not only by "competition" modeled as a latitudinal trend in "species saturation" (which is a special case of the implicit latitudinal gradient) but also by the effect of truncation applied on potential ranges and/or by the decreasing interspecific variance in potential extents toward higher latitudes (i.e., converging constraints; Figs. 4B and 5B). We could reveal these effects because we realized that causal mechanisms, such as those postulated by Stevens (1989), do not act on observed patterns but on underlying processes (here formation of potential ranges). Finally, the rescue or mass effect, which was denied by these authors, might increase alpha diversity (as predicted by Stevens) only up to the number of species considered in our models, which thus represent the local "species pool" of a site (rather than its regional diversity, which is generally defined as the number of ranges in a region without the necessity of their overlap; Brown and Lomolino 1998).

In conclusion, we have shown that the universal rules affecting potential or ideal entities (here, potential species' ranges) can have profound consequences on the patterns we measure in nature, which can themselves be strongly distorted by other effects. Proper testing of macroecological theories requires the exploration of all possible interactions of the theoretically assumed processes and potentialities with the intricacies of the real world.

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