RESEARCH PAPER

Latitudinal patterns of range size and species richness of New World woody plants

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ABSTRACT

Aim Relationships between range size and species richness are contentious, yet they are key to testing the various hypotheses that attempt to explain latitudinal diversity gradients. Our goal is to utilize the largest data set yet compiled for New World woody plant biogeography to describe and assess these relationships between species richness and range size.

Location North and South America.

Methods We estimated the latitudinal extent of 12,980 species of woody plants (trees, shrubs, lianas). From these estimates we quantified latitudinal patterns of species richness and range size. We compared our observations with expectations derived from two null models.

Results Peak richness and the smallest- and largest-ranged species are generally found close to the equator. In contrast to prominent diversity hypotheses: (1) mean latitudinal extent of tropical species is *greater* than expected; (2) latitudinal extent appears to be decoupled from species richness across New World latitudes, with abrupt transitions across subtropical latitudes; and (3) mean latitudinal extents show equatorial and north temperate peaks and subtropical minima. Our results suggest that patterns of range size and richness appear to be influenced by three broadly overlapping biotic domains (biotic provinces) for New World woody plants.

Main conclusions Hypotheses that assume a direct relationship between range size and species richness may explain richness patterns *within* these domains, but cannot explain gradients in richness *across* the New World.

Keywords
Dispersal barriers, diversity, geometric constraints, lianas, mid-domain effect, shrubs, trees.

INTRODUCTION

The latitudinal gradient in species richness is arguably the most important diversity pattern lacking a mechanistic explanation (Rohde, 1992; Rosenzweig, 1995; Willig *et al.*, 2003). This has led to an increasing number of hypotheses attempting to explain large-scale latitudinal richness gradients (Pianka, 1966; Wright, 1983; Rohde, 1992, 1999; Palmer, 1994; Rosenzweig, 1995; Brown & Lomolino, 1998; Dynesius & Jansson, 2000; Gaston &

Blackburn, 2000; Gaston, 2003; Storch *et al.*, 2005) that differ in mechanism(s) acting across different spatial and temporal scales (Latham & Ricklefs, 1993; Whittaker *et al.*, 2001; Willig *et al.*, 2003). Many clades have highest species richness near the equator with a somewhat regular decrease with distance from the equator (reviewed in Rosenzweig, 1995; Gaston, 2003; Willig *et al.*, 2003). As most diversity hypotheses are a posteriori explanations of this observed pattern, the mechanism(s) proposed are typically symmetric across the equator.

Latitudinal diversity hypotheses have traditionally been single-mechanism models that invoke a single global variable [e.g. climate variability (Janzen, 1967; Stevens, 1989), competition (MacArthur, 1972), temperature (Allen *et al.*, 2002), productivity (Currie, 1991), energy (Wright, 1983), etc.] acting continuously across latitudes to explain patterns of richness. More complex hypotheses argue for multiple mechanisms generating and maintaining latitudinal diversity gradients (Whittaker *et al.*, 2001; Hawkins *et al.*, 2003). These 'multiple-mechanism' models often argue for differential combinations of mechanisms that operate continuously across latitudes.

The idiosyncrasies and histories of places and clades may lead to the differential combinations of processes and/or to disconti-nuities in pattern and/or process across large scales. For example, large-scale dispersal barriers between biotic domains/provinces may generate breaks in pattern and/or process due to random effects (Colwell & Lees, 2000; Hubbell, 2001; Colwell *et al.*, 2004), independence of evolutionary histories (Latham & Ricklefs, 1993; Rosenzweig, 1995) and differences in geography or geological history (e.g. differences in areal extent; Rosenzweig, 1995).

In an effort to link mechanism with pattern, a central focus in biogeography and macroecology is to link diversity patterns with the forces that control geographical range size. For example, most of the prominent hypotheses attempting to explain the latitudinal diversity gradient assume, either explicitly or implicitly, that range sizes are central to understanding patterns of species richness (Stevens, 1989; Brown, 1995; Rosenzweig, 1995; Gaston & Blackburn, 2000; Whittaker *et al.*, 2001; Gaston, 2003). As many of the hypotheses linking range size with diversity patterns were raised to explain observed patterns, they predict a negative relationship between range size and richness. There are at least three prominent theories explicitly assuming a link between richness and range size.

First, Stevens' extension of Janzen's climate variability hypothesis asserts that a monotonic increase in temperature variance with latitude leads to a negative relationship between range size and richness (Janzen, 1967; Stevens, 1989). Furthermore, the 'evolutionary speed argument' posits that higher temperatures and faster generation times have led to higher speciation rates at low latitudes (Rohde, 1992, 1999; Allen *et al.*, 2002; Wright *et al.*, 2006). Thus, if 'new' species have smaller ranges than their ancestors, the correlation between latitude and temperature should generate a negative relationship between range size and richness.

Second, the differential extinction hypothesis argues that, at higher latitudes (especially northern latitudes due to Pleistocene glaciation; Brown, 1995), smaller-ranged species are more likely to have gone extinct, again leading to a negative relationship between richness and range size.

Third, 'mid-domain' null models (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Colwell *et al.*, 2004) demonstrate that richness gradients can be generated with the random placement of species ranges. Bounded, single-domain models (where species range limits do not exceed domain boundaries) should exhibit positive relationships between range size and richness. The domain centre can house the largest-ranged species coincident with the mid-domain richness peak. The exclusion of large-ranged species near domain barriers decreases both mean range size

and richness. While mid-domain randomizations typically use observed or theoretical range-size distributions to calculate expected values of species richness, they can also be used to calculate expected values of the mean and variance of range size.

If species richness is a continuous, unimodal correlate of latitude, and if patterns of range size are functionally coupled to patterns of richness, then the hypotheses above assert that range size will be a continuous, increasing, monotonic function of latitude. The strength and nature of this relationship under mid-domain models is a function of the range-size distribution observed and the domain limits assumed.

There is some empirical support for a positive correlation of latitude and range size. The pattern of smaller range sizes of tropical species ('Rapoport's rule'; Rapoport, 1982; Stevens, 1989) has been asserted for many taxa (Colwell & Hurtt, 1994; Brown, 1995; Gaston, 2003). The evidence of small tropical ranges comes from the high numbers of small-ranged endemics in tropical 'hot-spots' (Mittermeier *et al.*, 1998). In contrast to this evidence, several recent studies have noted tropical species with surprisingly large ranges (Pitman *et al.*, 1999; Condit *et al.*, 2002). Others have argued that there is, at best, a weak relation-ship between richness and range size (Gaston, 1999; Kerr, 1999; Gaston, 2003). Nevertheless, it is important to note that many studies of latitudinal richness and range size gradients have focused on extra-tropical regions (e.g. Stevens, 1989; Gaston, 2003; Hausdorf, 2006; Morin & Chuine, 2006), with few studies examining the *entire* terrestrial latitudinal gradient available to a taxon (e.g. Blackburn & Gaston, 1996; Lyons & Willig, 1997; Gaston *et al.*, 2005; Romdal *et al.*, 2005).

Here, we explicitly quantify the relationship between range size and local richness by examining the relationship between range size and richness of woody plant species across Western Hemisphere terrestrial latitudes by compiling one of the largest diversity and range-size data bases assembled for woody plants. Our goals here are to: (1) assess the relationship between range size and species richness across latitudes; (2) compare these rela-tionships with those expected by two classes of null models; and (3) compare our observations with several proposed explanations for the latitudinal gradients in species richness and range size.

Specifically, we use two measures of the central tendency and variance of range sizes to test and describe the functional relation-ship(s) between range size and richness across New World terrestrial latitudes. We show that hypotheses that assume a direct relationship between range size and richness may explain richness patterns but cannot explain gradients in richness *across* the New World.

METHODS

Data set

We generated a list of New World woody plant (i.e. trees, shrubs, lianas) species. The initial species list (3019 species) was taken from a series of New World woody plant inventories housed in the SALVIAS data bases (http://www.salvias.net/). We expanded this raw species list using field guides, regional lists and online data bases (*c.* 22,100 species). Using this species list we utilized
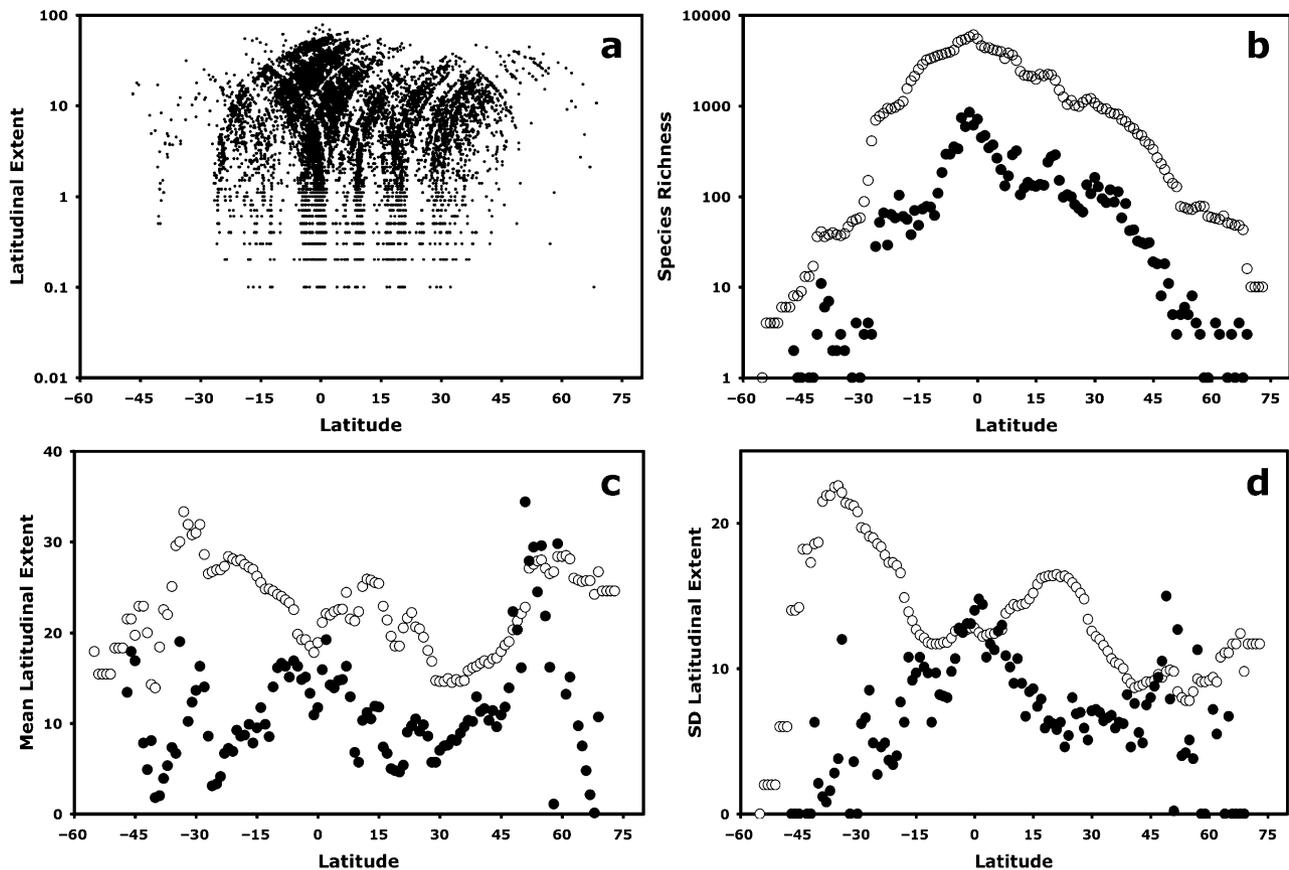
Figure 1 Observed values of richness and range size for 12,980 New World woody plant species. In this and all following figures negative values of latitude represent latitudes south of the equator. (a) Plot of the raw values of species mid-point and latitudinal extent, measured in degrees latitude. Latitudinal extent is scaled to $\log_{10}$ solely to show the smallest-ranged species. (b) Species richness by 1° latitudinal bin. Open circles are *S*, the count of all species found in that bin. Closed circles are *midS*, the count of all species with mid-points occurring in that bin. (c) Mean latitudinal extent by 1° latitudinal bin. Open circles are *MLE*, the mean for all species in that bin. Closed circles are *midMLE*, calculated only from the subset of species with a mid-point in that bin. (d) Standard deviation of latitudinal extent by 1° bins. Legend as in (c) above.

informatics tools accessible via the SALVIAS project to accumulate georeferenced point occurrences from online and in-house herbarium, inventory and atlas data bases (see Appendix S1 in Supplementary Material). Species represented by one sample location were removed from further analyses, as were morpho-species and incompletely determined specimens. Where possible, we removed cultivated species and specimens, corrected orthographic variants and standardized synonymy using regional floras and checklists, leaving *c.* 308,000 occurrences of 12,980 species with estimates of range extents (Fig. 1 and Appendix S2 in Supplementary Material). As far as we are aware, this is the largest collection of standardized range data assembled for woody plant species. We estimate that our species list comprises one-third to one-half of the total number of woody species within the New World.

We used two related methods to quantify richness and range sizes by 1° latitudinal bins. First, we calculated the total species richness (*S*), mean latitudinal extent (*MLE*) and standard deviation of latitudinal extent (*SDLE*) of all species that occur in a given 1° latitudinal bin (Stevens, 1989). Second, we calculated mid-point

richness (*midS*), mid-point mean latitudinal extent (*midMLE*) and mid-point standard deviation of latitudinal extent (*midSDLE*) of the subset of species with range mid-points that occur within that given latitudinal bin (Rohde, 1992).

Measures that allow species to be counted in more than one bin (hereafter 'overlap measures'; *S*, *MLE*, *SDLE*) are not independent across latitudes (Rohde, 1992). 'Mid-point measures', which include a subset of species present in a bin, may be biased by geometric constraints, where small-ranged species can have mid-points anywhere, while larger-ranged species are constrained to have mid-points near the middle of the domain (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Colwell *et al.*, 2004).

Null models

As both overlap and mid-point measures are imperfect, we compared observed measures of range size (*MLE*, *midMLE*, *SDLE*, *midSDLE*) with expected values taken from two null models that allow these range size measures to vary under simple

constraints. First, we used the 'standard' geometric constraint null model for two-dimensional data (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Colwell *et al.*, 2004). We generated uniform random mid-points and randomly assigned each a latitudinal extent drawn (with replacement) from the empirical distribution of latitudinal extents under the constraint that mid-point/extent combinations could not exceed the latitudinal constraints of 55° S and 75° N (i.e. the randomized range algorithm assigned a uniform random number > 0 and ≤ 1 multiplied by the distance to the nearest constraint boundary). This randomization procedure, hereafter referred to as the 'MDE null', addresses the question of how range size measures would be distributed given random location, but geometrically constrained, species ranges (Lyons & Willig, 1997; Willig *et al.*, 2003; Colwell *et al.*, 2004).

As our overall goal is to understand patterns of range size, given observed patterns of richness, we performed a second, more conservative, Monte Carlo randomization, hereafter referred to as the 'mid-point null'. Under the mid-point null, we randomly assigned latitudinal extents, drawn with replacement from that empirical distribution, to the empirical distribution of observed species mid-points. Thus, in the mid-point null, the observed and randomized distributions of mid-point species richness are identical. Our goal was not to randomize richness across latitude, as done in 'mid-domain' analyses (e.g. the model (2) null above; Willig *et al.*, 2003; Colwell *et al.*, 2004; Romdal *et al.*, 2005). The goal of the mid-point null randomization was to compare the observed range size measures with their expected values given the empirical distribution of mid-point richness.

Both randomization procedures shared the number of species ($n = 12,980$), number of iterations ($n = 100$), and geometric constraints (55° S and 75° N). We calculated randomized values of *S*, *MLE*, *SDLE*, *midMLE* and *midSDLE* by 1° latitudinal bin. We considered observed measures not different from expected values whenever at least 3 of 100 randomizations generated a higher value or at least 3 of 100 generated a lower value. Thus, we considered observed measures to be significantly different from expected only when the observed was greater than or less than 98% of the randomizations, corresponding to a $P \le 0.04$.

RESULTS

Species with the largest and smallest latitudinal extents had mid-points in the tropics (all 12,980 species are plotted in Fig. 1a). Few tropical species had mid-point/extent combinations that approached the geometric constraints assumed (i.e. 55° S and 75° N).

Observed patterns of richness and range extent

Species richness and mid-point species richness of the 12,980 New World trees, shrubs and lianas peaks at the equator (Fig. 1b) — matching latitudinal species richness gradients from numerous other taxa (e.g. Pianka, 1966; Rosenzweig, 1995; Willig *et al.*, 2003). Both $\log_{10} midS$ and $\log_{10} S$ are unimodal, best fit by quadratic polynomials (Table 1). While there has been considerable

debate about the best methods for quantifying richness across latitudes (mid-point versus overlap measures; see Stevens, 1989; Rohde, 1992; Gaston, 2003; Willig *et al.*, 2003), *midS* and *S* are highly correlated (standard linear regression, $r^2 = 0.76$; reduced major axis regression of $\log_{10} S$ and $\log_{10} midS + 1$ gives $r^2 = 0.90$).

Observed patterns of latitudinal extent are more complex than the pattern for richness (e.g. compare Fig. 1b and 1c). *MLE* across latitude is best fit by a cubic polynomial (Table 1) which shows a 'peak' (i.e. local maximum) at around 20° S, a 'trough' (i.e. a local minimum) around 40°N, and a monotonic increase north of 40° N. It is important to note that, for the latitudes reported in Stevens (30–75° N, Figure 1 in Stevens, 1989), we see the increase in *MLE* with increasing latitude originally reported by Stevens. The relatively independent measure *midMLE* is best fit by a quintic polynomial (Table 1, but note we did not assess the fit of higher than fifth-degree polynomials), which shows peaks at around 7° S and 56° N and troughs at 35° S and 27° N.

The variance of latitudinal extent when all species are considered (i.e. *SDLE*) is best fit by a quintic polynomial (Fig. 1d). However, *midSDLE*, where large-ranged species only affect the value of one bin, is unimodal as *midSDLE* across latitude is best fit by a quadratic with an equatorial peak.

In summary, species richness across latitude is unimodal with equatorial peaks. Measures of average range size across latitude are more complex. When bins are independent, the variance of range size (*midSDLE*) is unimodal with an equatorial peak.

Comparison of observations with null models

The results of the two null model randomizations are compared with observed values in Fig. 2(a)–(k). The conservatism of the mid-point null, relative to the MDE null, should be apparent from the broad intervals of values in regions of low species richness. At high levels of observed species richness, the expected values of *MLE* and *midMLE* from the randomization approach the mean of the observed range-size distribution. To simplify presentation of the results, we take the four comparisons in turn.

Mid-point measures and mid-point null

As the mid-point species richness (*midS*) in the observed data set is identical to *midS* in the mid-point null model, we do not plot observed and expected (but note, as a check, $r^2 = 1.00$). *MidMLE* is greater than expected by the mid-point null (red circles in Fig. 2d) in the north temperate (*c.* 50° N to 55° N) and around the equator (*c.* 10° S to 2° S and 1° N to 7° N). *MidMLE* is less than expected (yellow circles in Fig. 2d) around the southern limits of the tropics (21° S to 25° S), the northern limits of the tropics (16° N to 22° N) and northern subtropics (27° N to 34° N). The standard deviation of mid-point latitudinal extent (*SDmidLE*) is greater than expected at the equator. *SDmidLE* is lower than expected from Central America northward to the middle of the United States (13° N to 43° N), as well as the southern limits to the tropics (20° S to 26° S).

Table 1 Statistics for regressions of binned richness and binned range size against latitude. For each relationship we compare five models, linear to quintic polynomials. S is total species richness, $midS$ is mid-point richness, MLE is mean latitudinal extent of all species that occur in a given bin, $midMLE$ is the mid-point richness. 'Best-fit' model in **bold**. Model selection was based on ΔAIC which is the difference in AIC between a given model and the model with one less parameter. As we binned data by arbitrary distances (i.e. 1° latitude), and as bin values are not spatially independent, we do not report P values for these regression equations.

	Intercept	Linear	Quadratic	Cubic	Quartic	Quintic	r^2	AIC	ΔAIC
$Log_{10}\ S$	2.45	—	—	—	—	—	—	−6.12	—
	2.43	1.8×10^{-3}	—	—	—	—	0.004	−4.75	1.37
	3.47	**1.8×10^{-3}**	**-7.3×10^{-4}**	—	—	—	**0.928**	**−342.8**	**−338.1**
	3.57	-8.1×10^{-3}	-7.3×10^{-4}	3.8×10^{-6}	—	—	0.954	−403.3	−60.5
	3.66	-8.1×10^{-3}	-9.3×10^{-4}	3.8×10^{-6}	5.6×10^{-8}	—	0.960	−421.4	−18.1
	3.77	-1.9×10^{-2}	-9.3×10^{-4}	1.6×10^{-5}	5.6×10^{-8}	-2.6×10^{-9}	0.975	−481.2	−59.8
$Log_{10}\ midS$	1.50	—	—	—	—	—	—	−32.8	—
	1.50	-9.1×10^{-4}	—	—	—	—	0.001	−30.9	1.9
	2.35	**6.4×10^{-4}**	**-7.8×10^{-4}**	—	—	—	**0.840**	**−237.8**	**−206.9**
	2.40	-4.5×10^{-3}	-7.9×10^{-4}	2.5×10^{-6}	—	—	0.847	−241.7	−3.9
	2.54	-3.4×10^{-3}	-1.2×10^{-3}	1.8×10^{-6}	1.5×10^{-7}	—	0.872	−261.3	−19.6
	2.61	-9.6×10^{-3}	-1.2×10^{-3}	1.0×10^{-5}	1.7×10^{-7}	-2.3×10^{-9}	0.875	−263.7	−2.4
MLE	22.5	—	—	—	—	—	—	405.3	—
	22.5	1.6×10^{-3}	—	—	—	—	0.0002	407.2	−1.9
	21.9	1.6×10^{-3}	3.4×10^{-4}	—	—	—	0.012	407.7	−0.5
	23.7	**-1.8×10^{-1}**	**3.4×10^{-4}**	**7.1×10^{-5}**	—	—	**0.416**	**337.6**	**−70.1**
	22.1	-1.8×10^{-1}	4.3×10^{-3}	7.1×10^{-5}	-1.1×10^{-6}	—	0.515	314.3	−23.3
	23.1	-2.8×10^{-1}	4.3×10^{-3}	1.8×10^{-4}	-1.1×10^{-6}	-2.3×10^{-8}	0.563	301.8	−12.5
$midMLE$	11.4	—	—	—	—	—	—	414.3	—
	11.0	4.2×10^{-2}	—	—	—	—	0.04	410.4	−3.9
	10.8	4.2×10^{-2}	1.5×10^{-4}	—	—	—	0.03	412.3	1.9
	10.6	5.7×10^{-2}	1.8×10^{-4}	-8.0×10^{-6}	—	—	0.03	414.1	1.8
	9.3	4.7×10^{-2}	4.5×10^{-3}	-7.9×10^{-7}	-1.0×10^{-6}	—	0.07	410.5	−3.6
	13.55	**−0.33**	**2.7×10^{-3}**	**5.3×10^{-4}**	**-6.9×10^{-7}**	**-1.4×10^{-7}**	**0.43**	**356.1**	**−54.4**

AIC, Akaike information criterion.

Mid-point measures and MDE null

All observed mid-point richness values ($midS$) were less than expected by the MDE null north of 37° N, as were all but two values south of 11° S (Fig. 2a). Observed $midS$ from 9° S to 10° N was greater than expected by the MDE null. Overall, the MDE null was a poor predictor of observed $midS$ ($r^2 < 0.0001$ for both the linear regressions). The peak and trough structure for $midMLE$ observed in the mid-point comparison exists in the MDE comparisons (Fig. 2e). $MidMLE$ is greater than expected around the equator, the north temperate/boreal boundary (47° N to 64° N), and around 31° S and 46° S. $MidMLE$ is lower than expected by the MDE null across the northern (16° N to 34° N) and southern (16° S to 27° S) subtropics. The observed variance of latitudinal extent ($midSDLE$) is lower than expected by the MDE null across most of the latitudes examined here (Fig. 2i), with $midSDLE$ higher than expected at the equator.

Overlap measures and mid-point null

Species richness S and the range size measures mean latitudinal extent (MLE) and the standard deviation of latitudinal extent ($SDLE$) are calculated from all species that occur (or overlap) in a given latitudinal bin. While the mid-point null preserves $midS$, observed S, influenced by species with mid-points outside a given bin, varies from the mid-point null expectations (Fig. 2b). Thus S is higher than expected by the mid-point null over much of the tropics. Moving south from the northern boreal, MLE shows a regular decrease until it increases again around 28° N (Fig. 2f). MLE is significantly less than the expectation from 16° N to 55° N. Within the tropics, MLE increases with distance from the equator, but between 15° S and 15° N most MLE values are greater than expected by the mid-point null. The variance of latitudinal extent ($SDLE$) is lower than expected by the mid-point null for most of the north temperate region and the southern tropics (Fig. 2j) but greater than expected for most of the south temperate region and northern tropics.

Overlap measures and MDE null

The MDE null model shows a flat pattern of richness across most of the latitudinal gradient, as would be expected where the domain size is much greater than the mean of the range size frequency distribution (Fig. 2c). Observed species richness S showed a pattern similar to $midS$; there are more species in the tropics than expected by the MDE null and fewer than expected
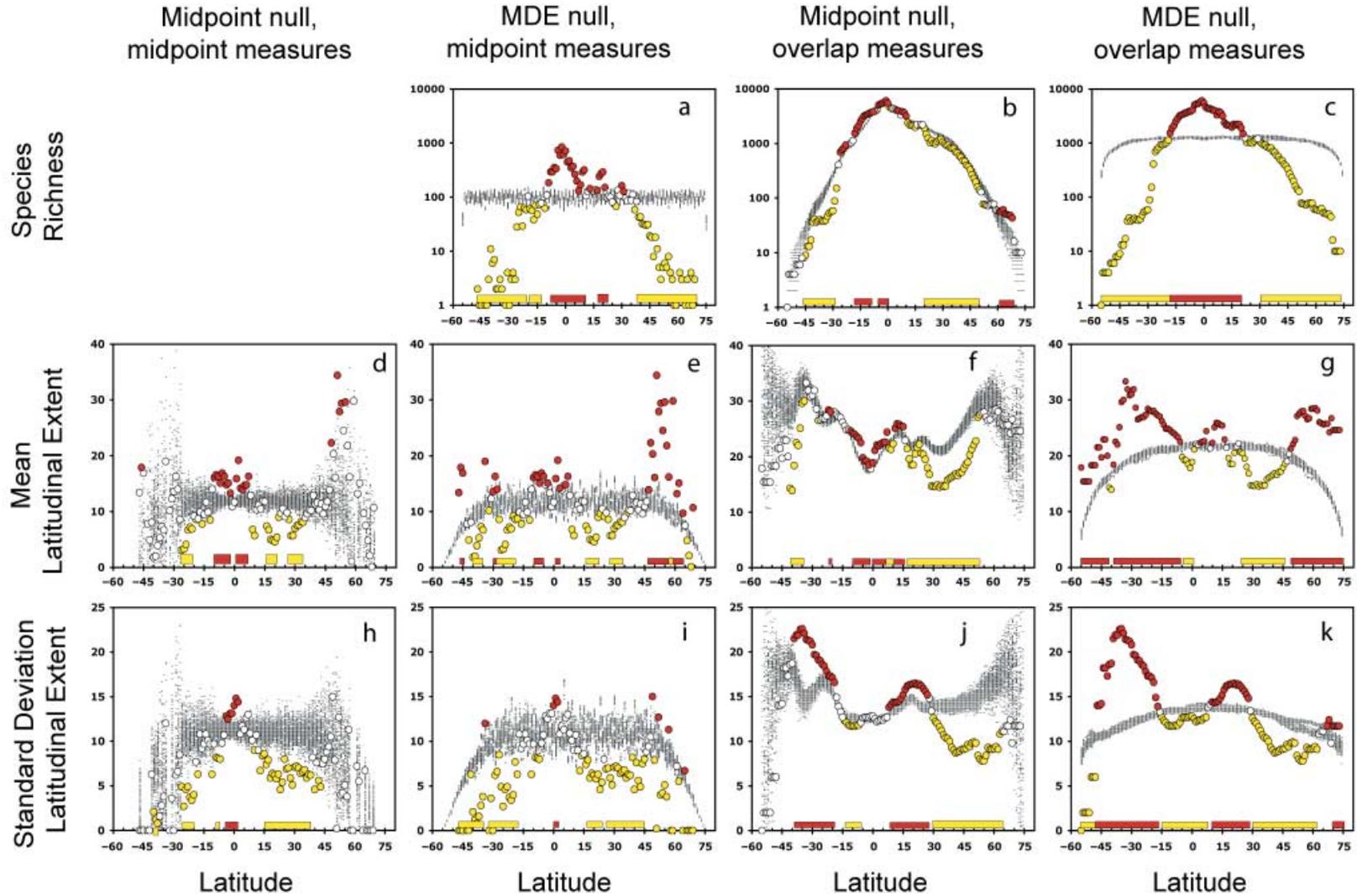
Figure 2 Comparison of species richness and range size variables to two null models. All results are binned by 1° latitude. Circles are observed values, dashes are expectations gained by 100 iterations of null models. Null models are mid-domain (i.e. 'box 5') and 'mid-point' (see Methods for details). Coloured circles show deviation from null expectations at $P = 0.04$, red circles are greater than expected, yellow less than expected, white circles are not different from the null model. Coloured bars along the ordinate axis represent significant ($P(run) < 0.05$) runs of greater than or less than expected where $P(run) = (n_{>or <exp}/N)^{run\,size}$. (a)–(c) Comparisons of species richness. Note that observed mid-point richness (*midS*) is identical to null expectations: (a) *midS* with expectations from MDE null; (b) *S* with expectations from mid-point null; (c) *S* with expectations from MDE null. (d)–(g) Comparisons of average latitudinal extent: (d) *midMLE* compared with mid-point null; (e) *midMLE* compared with MDE null; (f) *MLE* compared with mid-point null; (g) *MLE* compared with MDE null. (h)–(k) Comparisons of variance of latitudinal extent: (h) *SDmidLE* compared with mid-point null; (i) *SDmidLE* compared with MDE null; (j) *SDLE* compared with mid-point null; (k) *SDLE* compared with MDE null.
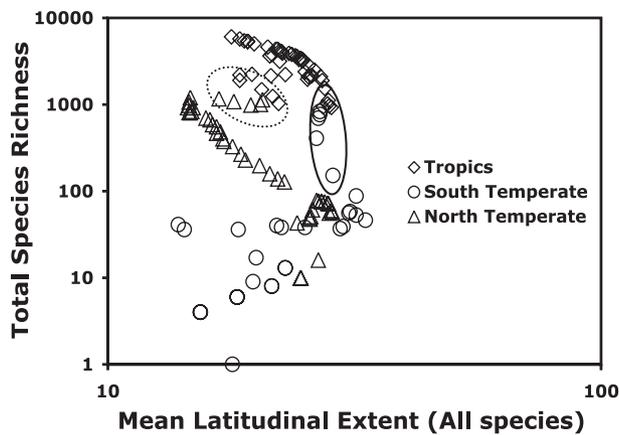
Figure 3 The relationships between $\log_{10} MLE$ and $\log_{10} S$ for tropical, south temperate and north temperate latitudes. All points included, there is no significant relationship between mean latitudinal extent and species richness ($r^2 = 0.006$, $P = 0.6442$). For the north temperate (triangles) there is a pronounced Rapoport effect [$\log_{10} S = 9.2 - (5.3 \log_{10} MLE)$; $r^2 = 0.69$, $P < 0.0001$] with higher richness associated with smaller range sizes. There is a less pronounced Rapoport effect for the tropics [diamonds; $\log_{10} S = 6.7 - (2.4 \times \log_{10} MLE)$; $r^2 = 0.33$, $P < 0.0001$]. The south temperate (circles) show a reverse Rapoport effect, with higher species richness associated with larger range sizes [$\log_{10} S = -3.8 + (3.9 \times \log_{10} MLE)$; $r^2 = 0.40$, $P < 0.0001$]. Temperate–tropical transitions are included in above regressions and marked with ovals to emphasize the discontinuities in the relationship (dashed oval 18° N to 28° N, other oval 18° S to 28° S). These discontinuities appear even though the points are not independent (i.e. both richness and mean latitudinal extent are spatially autocorrelated).

in extra-tropical areas (Fig. 2c). MLE was lower than expected by the MDE null from 17° N to 48° N and across the equator. With few exceptions MLE was greater than expected everywhere else. Observed SDLE was less than expected by the MDE nulls both across the equator and the north temperate to boreal (Fig. 2k) and greater than expected across most of southern South America and the northern subtropics.

Range size and species richness

Our analyses indicate that the relationship between MLE and species richness differs dramatically across the latitudinal gradient (Fig. 3). When all New World terrestrial latitudes are considered simultaneously, there is no relationship between latitudinal extent and species richness ($r^2 = 0.006$; Table S1 in Supplementary Material). However, when the data are analysed within regions (tropics, north temperate, south temperate, using tropical limits of 23° S and 23° N), a negative relationship between species richness and range size is observed within the north temperate (slope = −5.3, $r^2 = 0.69$, $P < 0.0001$) and the tropics (slope = −2.4, $r^2 = 0.33$, $P < 0.0001$), but not across the entire latitudinal gradient (Fig. 3). This is consistent with hypotheses that posit negative range size–richness relationships (e.g. climate variability, evolutionary speed, differential extinction) *within, but not across* these two regions. In contrast, the south temperate latitudes show

an opposite relationship, where richness is positively related to mean latitudinal extent (slope = 3.9, $r^2 = 0.40$, $P < 0.0001$). Thus, within the tropics and north temperate zones, increases in species richness are generated by the additional occurrence of small-ranged species, not due to increased overlap of large-ranged species. However, the slope of the latitudinal extent–richness relationship is steeper for the north temperate zone than the tropics. Furthermore, within the tropics, a given *MLE* yields approximately an order of magnitude more species than the same *MLE* in the north temperate zone.

In contrast to the above patterns, within the south temperate zone (55° S to 24° S), increases in richness are due to increased overlap of large-ranged species, not the addition of small-ranged species. The difference between north and south temperate areas may be due, in part, to the particular geometries of the two zones. As one moves south across the south temperate, decreasing continental area may preclude large ranges. The latitudinal band representing 55° N has approximately two orders of magnitude more species than 55° S, likely due to both larger longitudinal area (i.e. more mid-points) and overlap from species also found north of 55° N. Together, these patterns indicate that the processes that govern range size, and potentially richness, differ in magnitude and sign across latitude.

DISCUSSION

We present here what we believe is the most comprehensive examination of latitudinal trends in range sizes of woody plants in the New World. The equator is the location of both the greatest overlap of species ranges (i.e. highest *S*) and the greatest numbers of range mid-points (highest *midS*). Both *S* and *midS* are relatively monotonic functions of latitude (Fig. 1b & Table 1). Given the geometric constraints and data used here, species richness of tropical woody plants is greater than expected by the MDE null (Fig. 2a,c) as well as by our null model that holds mid-point species richness constant (Fig. 2b).

Neither measure of mean latitudinal extent is a monotonic function of latitude (Fig. 1c & Table 1). Quadratic models, concave-down and symmetric across the equator, explain 84% and 92.8% of the variance in $\log_{10} midS$ and $\log_{10} S$, respectively (Table 1). Hypotheses that assert a continuous relationship between range size and richness give expectations that cannot be reconciled with our observations. Rapoport's rule argues that *MLE* and *midMLE* will be concave-up, quadratic and symmetric across the equator. The quadratic models for *MLE* and *midMLE* explain 1–3% of the variance in mean extents.

While the largest mean range sizes occur outside the tropics, tropical *midMLE* is higher than in the subtropics and tropical *MLE* is larger than expected by chance. Within 10° of the equator, 16 of the 20 latitudinal bins have significantly greater *midMLE* and *MLE* than null model expectationss.

Rapoport's rule

While many have argued against the generality and/or existence of Rapoport's rule (Gaston *et al.*, 1998; Gaston, 1999; Kerr, 1999;

Rohde, 1999), recent studies have asserted that mean range size increases with distance from the equator for North American mammals (Arita *et al.*, 2005) and north temperate/boreal trees (Morin & Chuine, 2006). If only a portion of the terrestrial latitudinal gradient is examined (*c.* 25° N to *c.* 70° N; see Stevens, 1989; Morin & Chuine, 2006), Rapoport's rule appears to be correct (e.g. see those latitudes in Fig. 2f). The observation of a strong Rapoport signal for latitudes most affected by glaciation lends credence to the differential extinction hypothesis (Brown, 1995) that warrants further investigation. Given our data and results, Rapoport's rule is clearly not a general explanation of range size patterns. While Rapoport's rule may exist for some taxa for some regions (Gaston, 2003; Lomolino *et al.*, 2005; Morin & Chuine, 2006), the range size of these New World woody plant species is not a monotonic function of latitude.

The relationships between latitude and latitudinal extent do not match the unimodal predictions of Rapoport's rule, evolutionary speed or other hypotheses — including the 'mid-domain' null model examined here — that predict a monotonic relationship between richness and range size. While this failure to find a simple relationship between latitude and range size is sufficient to 'falsify' Rapoport's rule for these data, it is the nature and strength of the relationship between richness and range size that is of relevance to diversity hypotheses.

Mid-domain effect — how many domains?

The failure to match expectations of geometric constraint models is not surprising — even proponents of such models specifically argue against their utility at such large scales (Colwell *et al.*, 2004). The potential influence of geometric constraints on richness patterns within these temperate and tropical regions is not examined here. That said, as there is no latitude between 55° S and 75° N that can be considered a complete barrier to dispersal, the question then becomes, 'Where are the barriers to dispersal and recruitment across latitudes the strongest?'.

Our data suggest that the most stringent barriers to dispersal occur in the tropical to temperate transitions (*c.* 20° to 30° N and 20° to 30° S). *midMLE* is lower (Fig. 1c) and less variable (Fig. 1d) at these latitudes. Across these latitudes, *midMLE* is lower and less variable than expected, given observed values of species richness and geometric constraints (Fig. 2d,h). When overlap measures are used, the tropical–temperate transitions have higher variance than expected, which result from large-ranged species with range mid-points in the tropics or temperate zones overlapping with these smaller-ranged species. Our results suggest that this latitudinal gradient comprises at least three (but potentially more) overlapping 'leaky' biotic domains. Additional methods must be developed to objectively quantify and assess large-scale domain structure.

There has been much controversy about the use of geometric constraint models to calculate expected values of richness given an observed distribution of range sizes (Colwell *et al.*, 2005; Hawkins *et al.*, 2005). While we do not solve the controversy here, our analyses suggest additional ways of testing and/or quantifying mid-domain effects. 'Null' models of richness

patterns, generated by random placement of observed ranges, also yield expected values of central tendency and variance of range sizes (Fig. 2e,g,i,k), given a putative domain structure.

In summary, our results show that although species richness of New World woody plants is a unimodal correlate of latitude (Fig. 2a), the distribution of mean range sizes is more complex (Fig. 2b,c). Richness and range size show no consistent patterns across the entire latitudinal gradient. As a result, either there is no direct functional relationship between range size and species richness (as argued for mammals and insects by Kerr, 1999) or this relationship is discontinuous with latitude. These results simultaneously support the empirical, more regional findings of continental-scale studies of trees (Stevens, 1989; Morin & Chuine, 2006) and refute the latitudinal extrapolations made by Stevens (1989).

Our findings emphasize the danger of extrapolating diversity patterns from regional studies to broad-scale latitudinal gradients. The assumption that north temperate patterns continue into the tropics (and are symmetric across the equator) has been used to support hypotheses about tropical diversity (Stevens, 1989). Three patterns argue strongly for discontinuities in the ecological and evolutionary processes that influence variation in diversity and geographical range extents. First, patterns of mean mid-point latitudinal extents suggest 'troughs' around the limits of the tropics (*c.* 23° S and *c.* 23° N), possibly implicating stronger constraints on dispersal and recruitment across the subtropics.

Second, there are apparently three different relationships between range size and richness (Fig. 3). While the north temperate and tropical zones both show a negative relationship between range size and richness, the north temperate slope is much steeper, and north temperate richness an order of magnitude lower, than the tropics. The transitions in the range size–richness relationship are abrupt across both of the temperate–tropical transitions (see ovals in Fig. 3), and not simply the continuation of a single relationship.

Third, the range size–richness relationship shows opposite patterns for the north and south temperate zones. Together, these results show that the unimodal increase in species richness towards the equator cannot be driven by a unimodal pattern in range-size distributions.

It is important to acknowledge explicitly that we make no statistical corrections for sampling effort or area of a latitudinal bin in this analysis. A potential bias of the data would be that poorly sampled species (i.e. within the tropics) have their range sizes underestimated by the incomplete sampling of their entire species range. Given the species richness pattern in Fig. 1(b), and the latitudinal distribution of the number of observations (see Fig. S1 in Supplementary Material), the number of samples per species per bin is lowest near the equator. If lower per species per bin sample sizes underestimate latitudinal extents, this suggests that our analysis is biased towards finding smaller range sizes in the tropics, due to decreased sampling effort. Our results, however, indicate that, even with this potential bias, the latitudinal extents of tropical species are, on average, larger than expected. Additionally, our analysis is explicitly one-dimensional (i.e. latitude). It is possible that patterns of two-dimensional ranges

(i.e. latitudinal and longitudinal) fit expectations of Rapoport's rule and mid-domain models better. Future work will focus on extending our one-dimensional analysis to two dimensions.

Our results highlight a novel large-scale pattern that simultaneously supports apparent contradictions of tropical woody plant species range size — the tropics have numerous small-ranged endemics (Mittermeier *et al.*, 1998) as well as the largest-ranged species (Pitman *et al.*, 1999; Condit *et al.*, 2002). While richness is unimodal with latitude, New World woody plants may form three overlapping latitudinal domains (i.e. where dispersal potential is higher within subregions than between subregions) with smaller average range sizes in more xeric, subtropical latitudes – a potentially overlooked conservation priority. Empirical studies of latitudinal diversity often extrapolate regional analyses to hemispheric scales and assume that dispersal and recruitment probabilities vary monotonically with latitude. Our results paint a more complex picture — extrapolation of regional latitude–range size relationships to the entire gradient will give results incorrect in magnitude and sign. This is especially true across the xeric tropical–temperate transitions, which are likely to be strong barriers to dispersal by more mesic species.

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BIOSKETCH

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Statistics for regressions of latitudinal extents and species richness.

Figure S1 Number of observations in the analysis by latitudinal bin.

Appendix S1 Electronic data sources used in this analysis.

Appendix S2 Estimates of species latitudinal extents used in this analysis.

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