

THE INFLUENCE OF BAND SUM AREA, DOMAIN EXTENT, AND RANGE SIZES ON THE LATITUDINAL MID-DOMAIN EFFECT

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Abstract. Although the mid-domain effect (MDE) model for species richness in bounded geographical domains has proved controversial, several studies have revealed its explanatory potential for patterns of species richness. This paper investigates unexplored aspects of one-dimensional MDE, based on a data set of latitudinal distributions of New World birds (3706 species) on a 1° scale. Two previously published data sets for other taxa are also considered. We adjusted band sums (number of species per latitudinal band) for longitudinal area by constructing species–area curves for each band. Area-corrected richness patterns differed substantially from raw band sums, although both confirmed a strong, mid-tropical peak in richness. An MDE model accounted for 47% of the adjusted pattern, whereas area alone explained 13% of variation. Area-adjusted band sum data proved preferable to coastal transect data from the same data set. MDE was relatively more important in smaller latitudinal domains and/or for taxa with relatively large ranges. On fundamental grounds, we concluded that MDE randomizations based on empirical ranges are more appropriate than those based on theoretical range size distributions. Models that, like MDE, produce quantitative richness predictions should be evaluated statistically against the null hypothesis of equality, not simply correlation, of empirical vs. predicted richness values.

Key words: band sum area; birds; geographical domain extent; latitudinal gradient; Madagascar; MDE model; mid-domain effect; New World; randomizations; range size distribution; species–area curves; species richness.

INTRODUCTION

The foundations of the remarkable species richness of Earth's tropical biomes are still debated. Recent decades have brought many new proposals regarding mechanisms, but an extraordinary lack of consensus persists (e.g., Rohde 1992, Rosenzweig 1995, Gaston 1996, Kerr 2001, Willig et al. 2003). Among the currently favored explanatory factors are variables that relate to energy and productivity (Currie 1991), habitat heterogeneity (Hansson et al. 1995, Guégan et al. 1998), evolutionary processes (Rohde 1999), regional and evolutionary history (Ricklefs et al. 1999), area (Rosenzweig 1995), and synergism between climate and evolutionary history (Rahbek and Graves 2000, 2001, Jetz and Rahbek 2002). In addition, the potential role of geometrical constraints on species distributions has been emphasized by Colwell and Hurtt (1994). When boundaries confine species within a bounded *domain* (for example, a biome), random placement of ranges within the domain results in more overlap of ranges at mid-domain than elsewhere. This is termed the mid-domain effect, MDE (Colwell and Lees 2000a). Published models and analyses suggest that MDE often contributes significantly to latitudinal richness patterns, although the methodology in the studies

published so far varies considerably. Colwell et al. (2004) provide a full review of MDE studies to date.

The influence of area on species richness is undisputed and must be taken into account when analyzing other factors (Rosenzweig 1995, Rosenzweig and Sandlin 1997, Willig 2001). McCoy and Connor (1980) found considerable differences in latitudinal richness patterns of North American mammals depending on whether richness was expressed as the total number of species within each latitudinal band (*band sum*) or as the mean number of species within the quadrats composing each latitudinal band. They advocated the use of band sums in order to include the influence of longitudinal area, in the form of species turnover within latitudinal bands. Other studies of the latitudinal gradient of species richness (Willig and Sandlin 1991, Willig and Gannon 1997, Hawkins and Porter 2001, Koleff and Gaston 2001) have since incorporated area. Not adjusting for area variation (Willig and Lyons 1998) renders distinction between latitudinal and longitudinal patterns impossible (Bokma and Mönkkönen 2000, Jetz and Rahbek 2001).

In this paper we examine the relative importance of MDE, given the influence of area. By using large distributional databases of all terrestrial birds, marsupials, and bats of the New World and endemic mycalesine butterflies and birds of Madagascar, we furthermore explore two important features influencing the MDE on latitudinal gradients of species richness: (1) the in-

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fluence on MDE predictions of range size frequency distributions (RSFDs), whether theoretically or empirically derived, and (2) the influence on MDE predictions of the domain extent of the focal taxa, i.e., the degree to which the taxa under investigation, collectively, are distributed fully or only partially over the analyzed gradient.

The mid-domain effect has received much interest and has caused intensive debate (Bokma and Mönkönen 2000, Colwell and Lees 2000b, Jetz and Rahbek 2001, 2002, Koleff and Gaston 2001, Diniz-Filho et al. 2002, Hawkins and Diniz-Filho 2002, Laurie and Silander 2002, Zapata et al. 2003, Colwell et al. 2004, Pimm and Brown 2004). We refer the reader interested in details of that debate to the papers cited, rather than repeating arguments here. It is necessary to point out, however, that we consider geometric constraints to constitute a potential contributory influence on spatial patterns of richness. MDE models may be used not only to explore geometric constraints theoretically, but also when appropriately constructed, can provide a yardstick by which to assess the level of that influence in empirical settings. Although we endorse the consensus that geographic patterns of species richness and turnover have multiple causes/influences (e.g., Lawton 1996, Willig et al. 2003, Colwell et al. 2004), aside from examining the influence of area, we do not statistically assess competing explanations for geographic patterns (e.g., energy, topography). Our interest here is limited to exploring the explanatory potential of MDE for latitudinal patterns of species richness, in the context of varying longitudinal area and varying relationships between range size distributions and domain size.

EMPIRICAL DATA

New World bird data

The main data set, compiled for this paper, comprises the latitudinal distributions of New World birds. The New World is an eminently suitable geographical template for testing macroecological models (Blackburn and Gaston 1996a), especially those concerning latitudinal gradients of species richness, because the land mass spans a wide range of latitudes from the southern temperate zone over the equator to the northern temperate (and subarctic) zone. It is a discrete land mass semi-isolated from other land areas, resulting in a highly endemic flora and fauna: e.g., 95% of its terrestrial breeding birds are endemics to the New World (Blackburn and Gaston 1996a). The assemblage of birds of the Americas shows an extensive occupancy of the complete terrestrial latitudinal domain, with a remarkable 63 species in the northernmost band (at 72° N) and 101 species in the southernmost (54° S). Finally, the geographical ranges of New World bird species are also better known and the taxonomic inventory is more complete than for any other speciose group of organ-

isms (Rahbek and Graves 2001). The geographical domain was defined as continental North, Central, and South America excluding islands adjacent to the continent, e.g., Nova Scotia and Tierra del Fuego. We included all breeding species using terrestrial or coastal habitats (thus including such groups as waders and gulls). Species breeding only on cliffs or islets away from the shoreline or mostly depending on nonterrestrial/noncoastal habitat were excluded (i.e., mainly north temperate–polar region petrels, shearwaters, auklets, and skuas, but also tropicbirds).

We relied exclusively on the species-level taxonomy of Sibley and Monroe (1990, 1993), which reflects a “traditional” taxonomy, adding 25 newly discovered species as compiled by de By (2002). Latitudinal range extent for each species ($n = 3706$) was mapped at a resolution of 1° latitudinal bands. All ranges are treated as continuous. (This assumption is evaluated in Appendix B.) For North America we used the volumes of *The Birds of North America* (Poole and Gill 1992–2000), supplemented with ranges in Sibley (2000). For Central America we used Howell and Webb (1995), which covers Mexico to Nicaragua, supplemented with information from Stiles and Skutch (1989) and Ridgely and Gwynne (1989) for Costa Rica and Panama, respectively. Nicaragua is not yet fully covered by any authoritative work, but Howell and Webb (1995) and Ridgely and Gwynne (1989) in combination provide the information necessary for recognizing boundaries within that country. For South American birds we used the data set of Rahbek and Graves (2001; for details, see Fjeldså and Rahbek 1997, 1998). Historical ranges as well as ranges of extinct species were included if and when the necessary information was provided by the reference works. Exotic species ($n = 16$), found mainly in North America, were excluded.

Additional data sets

As an alternative approach to eliminating bias caused by variation in area of longitudinal bands, we constructed two line transects based on coastal distributions only. Coastal distributions, under oceanic climatic influence, were assumed to be more ecologically comparable over a broad latitudinal scope than data from inland transects. We used 1° latitude–longitude cells, but only species that actually reach the coast, as seen on the distribution maps, were included, which makes these data sets independent of variation in area of the cells. A variety of habitats apart from purely coastal environments were doubtless included, but species not known from low elevations were excluded. If more than one 1° cell contained coastline in a latitudinal band, the westernmost cell (for the west coast transect) or the easternmost cell (for the east coast transect) containing at least 50% land area was used. Consequently, the coastlines of the inner part of the Gulf of California and Gulf of Mexico are ignored in favor of the oceanic coastlines of Baja California and Florida.

To highlight the influence of range size, two taxonomic subsets were analyzed. Hummingbirds were singled out as a group with relatively small ranges. They include the smallest birds in the world and are remarkable for their spectacular evolutionary radiation, which has resulted in a clearly defined, speciose nectarivorous–insectivorous clade (Bleiweiss et al. 1997, Rahbek and Graves 2000). Raptors, as large-sized predators, are an obvious choice for a large-ranged taxon (for discussion of body size vs. range size, see, e.g., Blackburn and Gaston [1996a]). The two-dimensional distributions of raptors have previously been analyzed at a coarser scale for South America (Diniz-Filho et al. 2002).

We also reanalyzed data from two major latitudinal studies of MDE and species richness. Willig and Lyons analyzed a continental data set on marsupials and bats of the New World (details in Willig and Lyons 1998; also used by Willig and Gannon 1997, Lyons and Willig 1999, 2002), whereas Lees and co-workers analyzed a regional data set on birds and mycalesine butterflies of Madagascar (details in Lees et al. [1999]; also used in Lees [1996]). The two New World mammal data sets differ from the New World bird data gathered for this paper in that the domain extent of the focal taxa does not cover the entire landmass (i.e., unlike birds, neither bats nor marsupials occur all the way from Alaska to the southern tip of South America). The Madagascar domain shares some features with the New World data in being an extremely well-defined (and isolated) domain, but the latitudinal extent of the domain is much smaller and lies entirely within the southern hemisphere.

RESOLVING THE BAND SUM BIAS

With the exception of coastal transects, all of our analyses are based on *band sum* data, the total number of species whose ranges extend into a rectangular latitudinal band spanning the given land mass from west to east coast. The width of a New World latitudinal band is 1°. Although latitudinal gradients of richness are often calculated as band sums, such data are confounded by the effect of area (McCoy and Connor 1980, Jetz and Rahbek 2001), because the area of latitudinal bands depends upon the width of the domain, e.g., a continent (McCoy and Connor 1980, Willig and Sandlin 1991). Band area for the New World varies from 22 000 km² at the southern tip of South America to 575 000 km² in the broadest part of South America. Because bands vary so much in area, band sums of richness depend, in part, on longitudinal species turnover, which, to a first approximation, depends on band length. To investigate the contribution of species turnover to band sums, we performed analyses on band sum data as well as on data adjusted to the value expected for a standardized area, employing latitude-specific species–area curves (following Rahbek’s [1997]

approach for elevational gradients). The procedure for deriving these is detailed in Appendix A.

MID-DOMAIN EFFECT MODELS

We modeled the mid-domain effect (MDE) for one dimension by selecting “ranges” (line segments less than or equal to unit length) at random, with replacement, from a range–size frequency distribution (RSFD), placing each such range at random on a unit domain. Placement was constrained by the rule that no range may extend beyond the bounds of the domain. The application RangeModel (Colwell 2000) was used for these procedures. The RSFD describes the distribution of range sizes within the species pool (e.g., uniform, mostly wide-ranging species, or mostly narrow-ranging species). The empirical species pool has its own unique RSFD.

We analyzed each data set in relation to MDE prediction based on two models, defined by different RSFDs. The two models share the fact that predicted richness pattern is always a symmetric distribution with a mid-domain richness peak or plateau, falling to zero at the extremes, with steeper slope near the extremes than near the peak.

Random placement of empirical ranges (RER model).—In this model we used the empirical RSFD for a particular taxon in a particular domain to approximate the evolutionary and ecological potential RSFD for that taxon in that domain. By randomizing the placement on the domain of ranges drawn at random from the RSFD, we asked to what degree the empirical pattern of richness departs from the pattern expected, if the evolutionary and ecological events that produced the empirical location of ranges had done so independently for each species, and had done so without regard to environmental or historical gradients within the domain.

Random placement of theoretical ranges (RTR model).—In this model, the procedure was the same, but we ignored the empirical RSFD and instead used a purely theoretical RSFD that assumes (1) that range–midpoint combinations occur as a uniform random pattern in a bivariate range–midpoint plot (the “fully stochastic” model of Colwell and Lees [2000a]; see their Box 2); and (2) there is no lower limit on range size, and the upper limit on range size is equal to the full domain.

Although predictive models have thrived in population ecology and other disciplines, models that predict numbers of species are a relative novelty in biogeography, and they call for a change in testing methodology. Veech (2000) and Connolly et al. (2003) applied a stringent hypothesis-testing approach, testing the null hypothesis that MDE model outputs were not statistically different from empirical patterns. Tests of slope and intercept (e.g., Hawkins and Diniz-Filho 2002) or the test of probability density *P* of Laurie and Silander (2002) are de facto also testing for significant

TABLE 1. Basic statistics of all data sets.

Data set	Domain extent	No. species	RER mean range size	RTR mean range size
New World birds	126°	3706	21.2°	42.0°
West coast birds	125°	1257	14.9°	41.7°
East coast birds	124°	1729	18.5°	41.3°
Hummingbirds	126°	307	14.6°	42.0°
New World raptors	126°	96	42.2°	42.0°
New World marsupials	126°	82	17.2°	42.0°
New World bats	126°	253	29.0°	42.0°
Madagascar butterflies	12.5°	66	4.4°	4.2°
Madagascar birds	12.5°	134	10.7°	4.2°

Note: Mean range size for the RER model (randomized empirical ranges) equals the empirical mean range size, but mean range size for the RTR model (randomized theoretical ranges) is always 1/3 of the domain size.

deviation of MDE predictions. This approach generally reveals that MDE differs significantly from the richness pattern on a latitudinal domain, justifying the rejection of the null hypothesis that MDE fully accounts for the pattern of richness. Others (Willig and Lyons 1998, Lees et al. 1999, Jetz and Rahbek 2001, Koleff and Gaston 2001, Diniz-Filho et al. 2002, Hawkins and Diniz-Filho 2002, Sanders 2002) have emphasized the relative predictive power of MDE, represented by the r^2 of a regression. We follow the latter approach.

However, MDE model outputs are more than *correlates* of species richness (unlike variables such as temperature or altitude) for which we should attempt to maximize the fit (r^2) of an ordinary least squares (OLS) regression. In the appropriate context, they are *predictions* of actual richness, for which the accuracy of prediction can be evaluated by computing deviations from the “unity line” of slope 1 and intercept 0 (Poole 1974). The amount of variation explained (r^2) by the unity line is an adequate quantitative descriptor of how well the model has predicted the empirical species richness pattern. In this paper we apply, for the first time in this research field, both types of linear regression and compare the behavior of r^2 . We report r^2 values from ordinary least squares regression lines as OLS r^2 and r^2 values from unity line regressions as unity line r^2 . In unity line regression, when applying the standard formula for calculating r^2 ($r^2 = \text{regression ss} / [\text{regression ss} + \text{residual ss}]$), the residuals are simply the predicted minus empirical values for all data points. Unity line r^2 is thus easily calculated from typical statistical package output.

All RangeModel (Colwell 2000) outputs presented are from simulations involving 100 000 species. Richness values of simulations are adjusted to represent the average expected model output for a species assemblage of the given size.

RESULTS

The basic characteristics of the different data sets are outlined in Table 1. There are 3706 bird species in the Americas data set, of which 1257 are also in the transect following the west coast, and 1729 in the east

coast transect. The mean latitudinal range of a New World bird species (and thus, of model RER for these species) is 21.2 degrees of latitude, whereas the mean range of bird species in the coastal data sets is somewhat smaller. The mean range in model RTR is always exactly 1/3 of the domain length, a consequence of the uniform bivariate distribution of range–midpoint pairs (Colwell and Lees 2000a). In the New World bird data set, 1/3 of the domain is 42 degrees of latitude, twice as large as the mean of the empirical ranges. For the bird taxonomic subsets, hummingbirds, as expected, have small ranges and raptors have very large ranges. Of the mammal data sets, marsupials have relatively small ranges compared with bats.

We produced six species–area curves between 40° S and 56° N from the New World bird data set (Appendix A). Interpolations of the slope of the species–area relation, z , provided estimates of z for intervening latitudes. Subsequent application of the Arrhenius equation allowed calculation of richness for any given latitude and area (Appendix A). In the analysis we used a standardized area of 22 136 km², which is the smallest band area in our data set, as it is more appropriate to downscale richness for the wide bands than to extrapolate richness for the small bands to an area that they do not possess. The same latitude-specific z values were also applied to taxonomic subsets and to New World mammal data, on the assumption that the value of z is more influenced by the shape of the bands and latitude than by taxon differences.

The empirical species richness pattern for New World birds, using full latitudinal band sums, is shown in Fig. 1a. There is an obvious peak in richness in tropical South America south of the equator, where the widest bands of the continent are found, whereas the narrow bands of Central America have many fewer species. When area is standardized to 22 136 km² using the latitude-specific species–area curves, richness values are of course much smaller (Fig. 1b). The peak is now less marked and shifted slightly north of the equator toward Central America. The highest values lie between 4° and 8° N, a band near the northern tip of

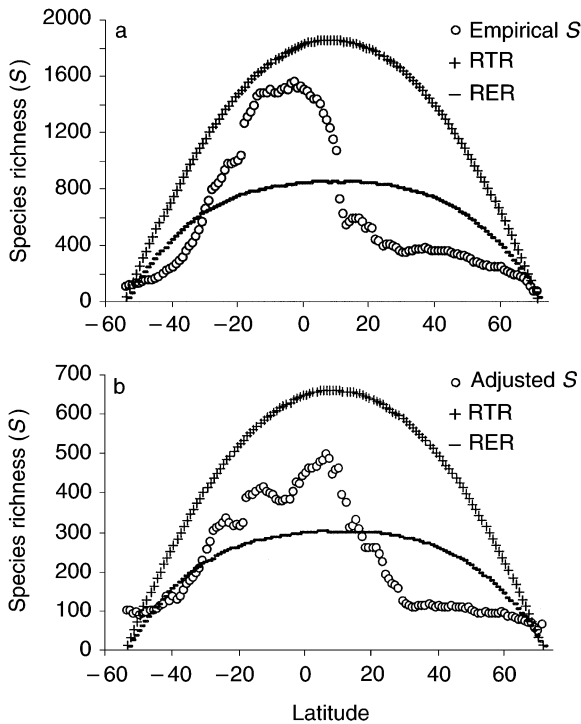


FIG. 1. (a) Comparison between the unadjusted empirical richness pattern (S) and model predictions for New World birds vs. latitude. The x -axis shows latitude from 60° S (-60) to 80° N. The RTR (randomized theoretical range) prediction is derived from a theoretical, bivariate uniform range size distribution function. The RER prediction is derived from a randomization of the empirical ranges. (b) Comparison between the area-adjusted empirical richness pattern (S) and adjusted model predictions for New World birds vs. latitude. The x -axis shows latitude from 60° S (-60) to 80° N. The empirical pattern is adjusted to an area of $22\,136\text{ km}^2$ for all latitudes, using latitude-specific species–area curves. The RER and RTR model predictions are the same as in panel (a), except that they are re-scaled to contain the same number of species as the adjusted empirical data set.

South America, crossing Colombia, Venezuela, and the Guianas. Between the equator and 10° S there is actually a slight richness depression before a quite gradual decline in richness through South America to the southern tip of the continent. There is a much steeper decline through Central America until 25° N, then a slow decline in North America. A general trend in the empirical patterns is that richness throughout North America is rather uniform compared with more pronounced changes within South America.

Predictions for the two models RER and RTR are compared with the unadjusted empirical pattern of Fig. 1a and with the area-adjusted pattern in Fig. 1b. The difference in magnitude of the two model outputs (RER vs. RTR) is caused by differences between the underlying range size frequency distributions (RSFDs). On the basis of OLS r^2 , model predictions conditionally explain approximately half of the latitudinal variation in the richness in New World birds, whether for raw

band sums or for area-adjusted empirical richness (Table 2). Although the OLS r^2 for RTR in both cases is slightly higher than for RER, the RTR values are actually much too great in magnitude, because RTR mean range size is much larger than RER mean range size. The RTR approach results in very low unity line r^2 in both cases (0.166 and 0.131), whereas, in contrast, the unity line r^2 of the area-adjusted empirical data on the adjusted output of RER is 0.471. In other words, MDE conditionally explains half of the variation in the area-standardized data.

In the west coast New World bird data set (Fig. 2a), a very pronounced peak is seen on the equator, coinciding with the occurrence of the Choco coastal forest in Ecuador and Colombia. Richness decreases in northern Chile (35° – 15° S), where the lowland habitat is mainly desert, and north of 24° N, where the coastal transect shifts from mainland Mexico to Baja California, which supports fewer species than the mainland. The east coast pattern is clearly bimodal (Fig. 2b). Each of the peaks is associated with a mountain chain approaching the coast (Serra do Mar and Serra dos Orgaos in Southern Brazil and the coastal Cordillera in Venezuela), presumably increasing topographical heterogeneity. As with Baja California, peninsular Florida (25° – 30° N) has fewer species than surrounding latitudes. The two coastal data sets are clearly more idiosyncratic than the main data set, and MDE explains at the most 37% of variation for unity line r^2 (Table 3). Again there is a clear discrepancy for OLS and unity line r^2 for RTR, but not for RER.

The taxonomic data subsets are also quite idiosyncratic. The RTR prediction, using a theoretical RSFD, produces a visually more accurate prediction for the raptor subset (Fig. 2c) than it does for the other subsets, because, by coincidence, raptors have the same average range size as the RSFD for this model. The two model outputs are thus very similar, but not identical, because the RSFDs differ in detail. The relatively high values of r^2 are therefore similar for both types of regression. Because hummingbirds (Fig. 2d) have small empirical

TABLE 2. Potential explanatory power of MDE (mid-domain effect) models on the empirical pattern of New World bird species richness, not adjusted for spatial autocorrelation.

Observed richness	MDE model	OLS r^2	Unity line r^2
Band sums	RTR	0.483	0.166
Band sums	RER	0.434	0.430
Area-adjusted	RTR	0.545	0.131
Area-adjusted	RER	0.474	0.471

Notes: The two models, RER and RTR (random empirical or theoretical ranges, respectively), are applied to both raw latitudinal band sums and to area-adjusted latitudinal band data. Two types of regression are performed: OLS (ordinary least-squares) and “unity-line” regression (see *Testing model predictions* for details). All regressions are significant at $P = 0.05$.

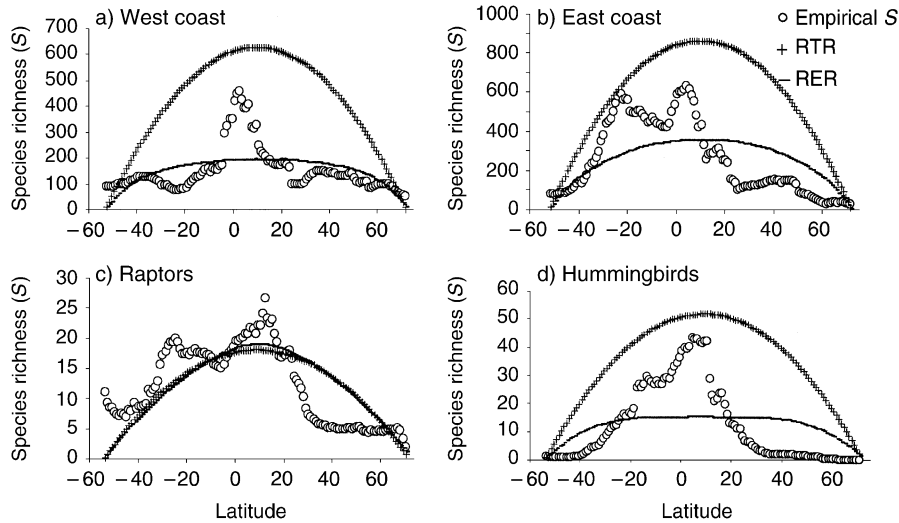


FIG. 2. Latitudinal species richness pattern vs. latitude for coastal data sets and for taxonomic subsets of the New World bird data set. The x-axis shows latitude from 60° S (−60) to 80° N. Empirical species richness is in all cases compared with RER and RTR model predictions. Taxonomic subsets are area-adjusted.

ranges relative to the domain, the RER model produces a relatively flat-peaked curve (Colwell and Hurtt 1994), whereas RTR (as always) is parabolic. The RTR OLS r^2 for hummingbirds is 0.5, but the magnitude is consistently much too high, and the unity line r^2 for RTR is thus very small. The RER values for hummingbirds are lower than for raptors, but robust to type of regression.

Fig. 3 and Table 4 present reanalysis of patterns of distribution of New World mammals as well as data from Madagascar birds and butterflies. The comparisons of unadjusted band sums for marsupial and bat species richness with RTR model predictions are identical to results in Willig and Lyons (1998). Adjusting for area bias improves values marginally. OLS r^2 in all cases is slightly higher for RTR than for RER, but the explanatory power of RTR in the unity regression is very poor for marsupials. The percentage of variation explained for the bats, which have much larger ranges, on average, than marsupials, is quite high and relatively robust to regression type. The Madagascar data in general have very high r^2 values, indicating a strong influence of MDE in the pattern.

DISCUSSION

Richness patterns

That bird species richness increases toward tropical latitudes already has been demonstrated for North America by, for example, Cook (1969) and MacArthur (1969), and the pattern for the entire hemisphere has been described on a coarse scale by Blackburn and Gaston ([1996b]; equal-area grids of 611 000 km²) for all birds, and by Koleff and Gaston ([2001]; 5° scale) for parrots and woodpeckers. Our data set, the first to adjust for band sum area using species–area curves,

generally confirms the overall pattern described by previously published studies, but reveals noteworthy new details.

It is especially interesting that the absolute peak in species richness shifts slightly to the north when area is adjusted for. Meanwhile, there is quite an abrupt decrease in species richness when moving into North America. This probably reflects the periodic isolation of the major New World landmasses, with the Isthmus of Panama finally established only by mid-Pliocene (about 4×10^{-6} years ago; Pitman et al. 1993). North America has thus for long periods had a separate evolutionary history, resulting in much lower levels of species richness. The apparent dip in species richness just south of the equator (Fig. 1b) was first demonstrated by Rahbek and Graves (2001), who showed, on a two-dimensional grid, that the Amazon basin supports fewer bird species per $1^\circ \times 1^\circ$ grid cell than surround-

TABLE 3. Tests of RTR and RER model predictions for different subsets of the New World bird data set.

Subset	MDE model	OLS r^2	Unity line r^2
West coast birds	RTR	0.346	0.020
West coast birds	RER	0.252	0.251
East coast birds	RTR	0.398	0.084
East coast birds	RER	0.373	0.369
Raptors	RTR	0.485	0.476
Raptors	RER	0.517	0.507
Hummingbirds	RTR	0.507	0.124
Hummingbirds	RER	0.330	0.305

Notes: The west coast and east coast data sets are not area-influenced. For raptor and hummingbird subsets, tests are made on area-adjusted patterns only. The species–area curves derived from the main data set were applied. Details are as in Table 2. All regressions are significant at $P = 0.05$.

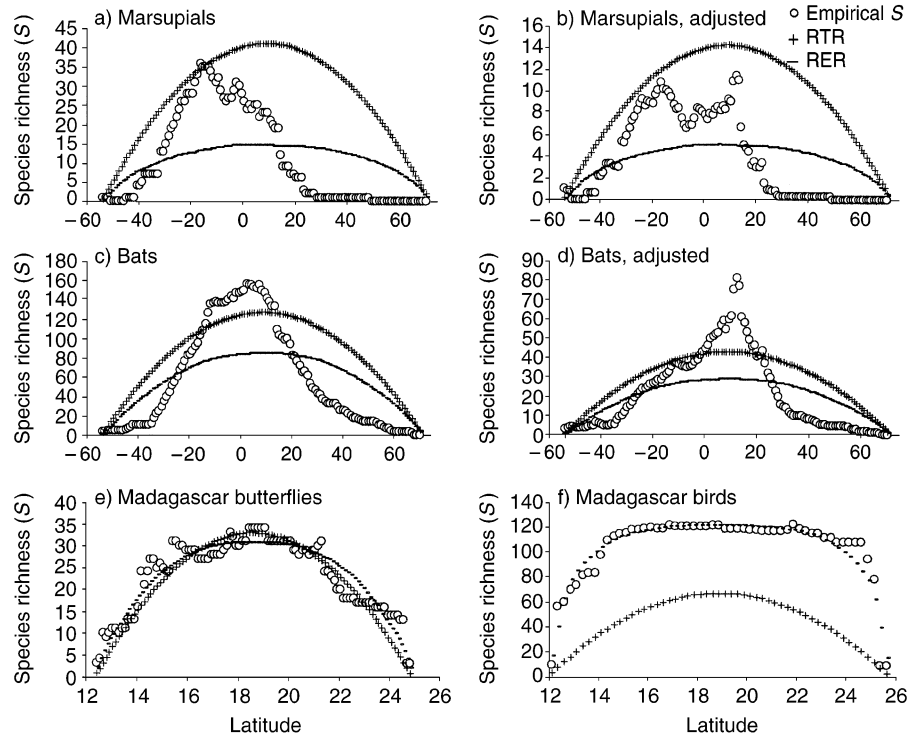


FIG. 3. Latitudinal species richness patterns for additional data sets and model predictions. (a–d) New World mammals, unadjusted vs. area-adjusted patterns for marsupials and bats. The *x*-axis shows latitude from 60° S (–60) to 80° N. The species–area curves derived from the main data set were applied. (e–f) Madagascar data for mycalesine butterflies and endemic birds. The *x*-axis shows latitude from 12° S to 26° S.

ing, more topographically heterogeneous regions. This pattern is strong enough to surface even in the area-adjusted, one-dimensional latitudinal domain, and it also appears in our raptor subset (Fig. 2c), confirming the findings of Diniz-Filho et al. (2002) for two-dimensional distributions. It is seen clearly even in the east-coast transect, which has its obvious peaks in the mountainous regions north and south of eastern Amazonia, and supports the idea of habitat diversity and/or topographic heterogeneity as generators of high regional species richness in the tropics (Kerr and Packer 1997, Rahbek and Graves 2001, Jetz and Rahbek 2002). The west-coast and east-coast transects of our study were analyzed under the assumption that they are more homogeneous than band sum data, in the sense that they are not influenced so much by longitudinal habitat variation. However, the regional variation within the transect patterns (Fig. 2a, b) is in fact more pronounced because they are more influenced by latitudinal variation in topography and climate. In South America, the west coast transect is under the influence of the cold Peru current, which results in extremely low values of richness south of the equator compared to the east transect. Probably, transects in general are not preferable to area-corrected band sum data for assessing broad latitudinal patterns. When fine-scale and/or multidimensional data are being analyzed, the amount of in-

formation on patterns is increased, but at the expense of simplicity. For instance, much of the information contained in two-dimensional species richness data sets concerns variation in species richness within latitudinal bands or zones, which does not necessarily contribute to answering the question of what causes the tropical peak in latitudinal richness, a one-dimensional pattern,

TABLE 4. Tests of RTR and RER model predictions for New World mammal data sets and on data for butterflies and birds from Madagascar.

Data set	MDE model	OLS r^2	Unity line r^2
Marsupials, band sums	RTR	0.354	0.110
	RER	0.329	0.308
Marsupials, area-adjusted	RTR	0.385	0.105
	RER	0.351	0.330
Bats, band sums	RTR	0.676	0.536
	RER	0.651	0.583
Bats, area-adjusted	RTR	0.639	0.511
	RER	0.605	0.549
Madagascar butterflies	RTR	0.897	0.838
	RER	0.886	0.883
Madagascar birds	RTR	0.690	0.319
	RER	0.910	0.870

Notes: Details are as in Table 2. All regressions are significant at $P = 0.05$.

by definition. It seems therefore that analysis of one-dimensional domains will still have a role to play in advancing our knowledge in macroecology (see also Colwell and Lees 2000b, Willig et al. 2003, Colwell et al. 2004).

Our analyses confirmed the clear mid-latitude peak found in Madagascar faunas by Lees et al. (1999). Because all points in Madagascar lie south of the equator, the strong Madagascar mid-domain peak contradicts traditional climatic explanations for gradient richness patterns, as shown by Lees et al. (1999) for a series of alternative hypotheses that failed to fit the data. The Madagascar domain has only about 1/10 of the extent of the Americas, but the empirical ranges of birds and butterflies are not proportionally small. For Madagascar birds, the RER model thus demonstrates extremely good fit, whereas in data sets with more narrow-ranging species (west coast New World birds, New World hummingbirds and marsupials), the fit of both RTR and RER is rather poor. Hummingbird distributions are much more concentrated in the mid-tropics than expected from MDE hypothesis for species with such small ranges (Fig. 2d). Their tropical richness peak is probably significantly related to history, as they are a group with a relatively recent explosive radiation (Rahbek and Graves 2000). The tropical origin of the group and recent expansion to most of North America mean that hummingbird diversity is still very much concentrated around tropical latitudes; their expansion seems not to be constrained by hard boundaries. In this respect they are similar to marsupials ($r^2 = 0.33$), but these are an old lineage whose distribution apparently has been diminished by subsequent invasion of placentals (Willig and Gannon 1997). Marsupials are now nearly absent in North America, which is occupied by a single species only (Lyons and Willig 1999). The pattern for Madagascan birds is unusual because it is a plateau with sharp drop-off of richness near the extremes. This shape is caused by the very large range sizes, relative to the domain. Unity line r^2 for RTR is a modest 0.32, because RTR in this case assumes smaller ranges, the opposite situation as with the hummingbirds or marsupials in the New World data sets.

Raptors, with larger range sizes than hummingbirds, show a better fit to MDE predictions than these (Fig. 2c, $r^2 = 0.51$). Speciation among raptors is believed to be based on large-scale vicariance, whereas many hummingbirds have speciated in tiny, presumably climatically stable areas along the Andes mountain chain (Fjelds  1994). What remains to be assessed in such cases as raptors is how much deviation from the general pattern is possible if other important factors act in strong contrast to MDE expectations. For the two-dimensional pattern of raptors in South America alone, Diniz-Filho et al. (2002) found little accord with MDE predictions. This indicates that longitudinal, intercontinental richness variation is largely determined by localized factors, rather than by MDE. In the case

of raptors, their two-dimensional distribution patterns in South America seem to be governed by habitat type (Diniz-Filho et al. 2002). In general, subgroups are more likely to exhibit departure from null model expectations for historical or biogeographical reasons than higher level, more speciose taxa, for which these factors are averaged out (see also Lyons and Willig 1999, Colwell and Lees 2000a).

Testing fit of models

We recommend that MDE models be based on re-sampling of empirical RSFDs (RER), rather than on theoretical RSFDs (RTR), which often have, at best, only coincidental relevance to particular taxa. Our tests show that the r^2 values of RTR models are much lower when tested against unity (unity line r^2) than in least squares regressions, because the magnitude of an RTR output is arbitrary. In contrast, the expected total graph area under an RER curve is always identical to the area under the corresponding empirical richness curve. For this reason, the decrease in r^2 from fitting a unity line regression instead of an OLS regression line is less dramatic. Randomization of empirical ranges does not constrain an MDE model to resemble the empirical richness pattern, contrary to speculation (Koleff and Gaston 2001, Hawkins and Diniz-Filho 2002, Zapata et al. 2003). Our RER evaluations, even where both empirical and model patterns had mid-domain peaks, resulted in r^2 values as low as 0.25, and other studies report even lower values (e.g., Sanders 2002, Diniz-Filho et al. 2002).

The importance of MDE models

Influence of MDE has been statistically demonstrated in a number of regional- and continental-scale studies (e.g., Willig and Lyons 1998, Lees et al. 1999, Jetz and Rahbek 2001, Koleff and Gaston 2001) and also in recent quantitative elevational studies (Sanders 2002, Bachman et al. 2004, McCain 2004). The results of this study support the hypothesis that distribution of species ranges may be influenced by geometric constraints (Colwell and Hurtt 1994, Colwell and Lees 2000a). The potential explanatory power of MDE in most cases was obvious, whereas the influence of area on the New World data sets and on the importance of MDE was surprisingly limited (an OLS regression with area as determinant for New World birds results in a modest r^2 of 0.13). At this large scale, sample area seems to be overshadowed by other factors (Willig and Sandlin 1991, Koleff and Gaston 2001). Small latitudinal domains and/or species with large ranges are more likely to produce a mid-domain effect (Colwell and Hurtt 1994, Lees et al. 1999, Jetz and Rahbek 2002). This means that we should expect stronger effects of MDE in patterns of species richness for small study regions or geographically small-scale gradients, such as most elevational gradients (see also Laurie and Silander 2002).

Finally, we recommend that assessment of the absolute fit of MDE models (and other models that predict species richness in units of species) evaluate model output in relation to empirical data as we have done here, by measuring residuals with respect to the unity line. It is inappropriate to inflate measures of fit for a predictive model by fitting data to the OLS regression line. Other hypotheses in the field of geographical species richness are currently developing predictive models (e.g., Bell 2001, Allen et al. 2002) and the relative influence of such competing hypotheses will be readily assessed by direct comparison of measures of fit from unity line regressions. However, most currently favored hypotheses (e.g., area, energy, habitat heterogeneity) are thus far expressed only as correlative variables for which model predictions of patterns of richness are not available. This renders unbiased comparative evaluation difficult. When assessing the importance of many factors simultaneously, in multiple or partial regressions or comparison of univariate regressions, one must enter predictive models such as MDE on equal terms as other factors.

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APPENDIX A

A description of resolving the band sum area bias is available at ESA's Electronic Data Archive: *Ecological Archives* E086-012-A1.

APPENDIX B

A test of the assumption of continuous ranges is available in ESA's Electronic Data Archive: *Ecological Archives* E086-012-A2.