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The Mid-Domain Effect and Species Richness Patterns: What Have We Learned So Far?

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ABSTRACT: If species' ranges are randomly shuffled within a bounded geographical domain free of environmental gradients, ranges overlap increasingly toward the center of the domain, creating a "mid-domain" peak of species richness. This "mid-domain effect" (MDE) has been controversial both in concept and in application. Empirical studies assess the degree to which the evolutionary, ecological, and historical processes that undeniably act on individual species and clades produce geographical patterns that resemble those produced by MDE models. MDE models that resample empirical range size frequency distributions (RSFDs) balance the risk of underestimating and overestimating the role of MDE, whereas theoretical RSFDs are generally biased toward underestimating MDE. We discuss the inclusion of nonendemic species in MDE models, rationales for setting domain limits, and the validity of one- and two-dimensional MDE models. MDE models, though null models, are not null hypotheses to be simplistically rejected or accepted. They are a means of estimating the expected effect of geometric constraints within the context of multiple causality. We call for assessment of MDE on an equal statistical footing with other candidate explanations for richness gradients. Although some critics have categorically dismissed MDE, an overview of the 21 MDE studies published to date reveals a substantial signature of MDE in natural patterns and justifies continued work.

Keywords: diversity and species richness gradients, domain limits, geometric constraints, mid-domain effect, null models, range size frequency distributions.

Geographic gradients in species richness have long been of interest to biogeographers (von Humboldt 1807; Wallace 1878), ecologists (Warming 1909), and evolutionary biologists (Dobzhansky 1950) and have been hypothesized to reflect underlying geographical gradients in a great variety of ecological and evolutionary factors (MacArthur 1965, 1972; Pianka 1966; Currie 1991; Rohde 1992; Palmer 1994; Brown 1995; Rosenzweig 1995; Gaston and Blackburn 2000; Whittaker et al. 2001). However, species richness gradients can also arise through simple geometric constraints on species range boundaries in the absence of any environmental or historical gradients. In either one or two dimensions, random placement of species geographic ranges on a bounded map produces a peak of species richness near the center, the "mid-domain effect" (MDE; Colwell and Hurtt 1994; Colwell and Lees 2000*a*; Jetz and Rahbek 2001).

Before the advent of MDE theory, biologists worked under the unstated assumption that species richness should be spatially uniform in the absence of environmental and historical gradients. If we accept the proposition that the biology of populations imposes some degree of spatial cohesion (aggregation) on the geographic ranges of individual species, then the traditional assumption of an underlying spatial uniformity of richness must be replaced with the expectation of a mid-domain richness peak or plateau. Therefore, existence of a mid-domain peak in empirical data sets is not in itself sufficient evidence that climatic or historical gradients are entirely responsible for the pattern. However, assessing the role of MDE in nature has proven technically and intellectually challenging. For this reason and because it questions the traditional view, MDE has proven controversial (Bokma and Mönkkönen 2000; Brown 2001; Koleff and Gaston 2001; Hawkins and Diniz-Filho 2002; Laurie and Silander 2002; Zapata et al. 2003).

In this article we first outline the basis and assumptions of MDE models, addressing critiques of MDE and prospects for further research. We explain that some criticisms of MDE apparently arise from misunderstandings of the nature of null models or of MDE models in particular.

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We also address other issues raised in studies of MDE, including causality, model dimensionality and design, domain definition, nonendemic species, discontinuous ranges, statistical assessment, and the issue of hypothesis-testing versus estimation of effect size. We then evaluate the results from the 21 empirical studies of MDE published to date. We conclude that MDE is prompting productive new ways of looking at biogeographical patterns and that the evidence reveals a substantial signature of MDE in natural patterns.

What Are Mid-Domain Effect Models, and What Do They Show?

MDE models are null models. In contrast with simulation or analytic models, which attempt to mimic reality, null models deliberately exclude some factor or mechanism of interest, providing a baseline for comparison with actual data sets (Harvey et al. 1983; Colwell and Winkler 1984; Gotelli and Graves 1996; Gotelli 2001). The importance of the excluded factor is then evaluated by the degree of mismatch between the data and the patterns predicted by the null model. The Hardy-Weinberg equilibrium is a familiar null model in population genetics: selection and other evolutionary forces (mutation, migration, meiotic drive, and genetic drift) are intentionally excluded by generating genotype frequencies expected through random mating and then evaluated by comparing these predicted frequencies with empirical ones (Hartl 2000).

The ideal null model is one that excludes only the "factor or mechanism of interest" while incorporating, as realistically as possible, other influences that might otherwise confound the results (Colwell and Winkler 1984 and many examples in Gotelli and Graves 1996). As in any model, additional factors that have no bearing on the outcome are best not incorporated at all. Null models have a long history in community ecology and biogeography (Gotelli and Graves 1996) and are now a well-established (though still debated) analytical tool (Gotelli 2001). See appendix A for further discussion of the history of null models in relation to MDE models.

In the case of MDE null models, the factor of interest that we attempt to exclude is any effect of spatial gradients on the distribution of species' range locations within a geographical domain. Examples include climatic gradients such as geographical patterns of potential evapotranspiration (Currie and Paquin 1987), temperature (Turner et al. 1987), or productivity (Kaspari et al. 2000); water-energy dynamics (e.g., O'Brien 1998); physiographic gradients such as degree of topographical complexity (e.g., Kerr and Packer 1997; Rahbek and Graves 2001); and historical "gradients" such as time since last glaciation for different points in space (e.g., Rabenold 1993; Graham et al. 1996). What MDE models specifically do not exclude is just as crucial a part of their design. Populations, individually, are assumed to retain their natural spatial structure (population cohesion) and thus their empirical frequency distribution of geographical range sizes.

In two dimensions, if polygons (representing geographic ranges) are randomly placed within a bounded area (for example, on the map of a continental area, for terrestrial species), a peak of polygon overlap (species richness) is produced near the center of the area (Ney-Nifle and Mangel 1999; Bokma et al. 2001; Jetz and Rahbek 2001, 2002; Diniz-Filho et al. 2002; Hawkins and Diniz-Filho 2002; Laurie and Silander 2002). The polygons may be irregular and concave in shape, produced by algorithms (such as the "spreading dye" model of Jetz and Rahbek [2001]) that explicitly model the spread of a species geographic range in a gridded coordinate space according to a specified algorithm. In one dimension, random placement of line segments (representing geographic ranges) between domain boundaries (e.g., between latitudinal, elevational, or bathymetric limits) produces a hump-shaped pattern of segment overlap counts (species richness; Colwell and Hurtt 1994; Pineda and Caswell 1998; Willig and Lyons 1998; Lees et al. 1999; Colwell and Lees 2000*a*; Veech 2000; Koleff and Gaston 2001; Grytnes and Vetaas 2002; Laurie and Silander 2002; Sanders 2002; McCain 2003). Every author, including critics, who has examined MDE models (table 1) has confirmed these facts. Laurie and Silander (2002, p. 351), for example, conclude that the mid-domain effect "is qualitatively a property of all biologically realistic null models based on range overlap counts." Appendix B ("An Analogy for Explaining MDE") offers an alternative way to visualize and understand MDE.

In MDE models, stochastic geometric phenomena produce nonuniform patterns of species richness within a bounded spatial domain. Because the boundaries are essential, such patterns may be said to be caused by geometric constraints (Colwell and Hurtt 1994; Pineda and Caswell 1998) or by edge effects (Laurie and Silander 2002), although it would be more accurate to say that the patterns are caused by stochastic processes operating within geometrically constraining boundaries.

Population Processes versus Biogeographic Patterns

Empirical species richness patterns are geographical epiphenomena of processes acting at the level of species or populations. The geographical distribution of any real species is not biologically random but instead is driven by complex and idiosyncratic interactions between real genes and real environments (including other species) shaped by historical contingency (Holt 2003). Likewise, patterns of speciation and extinction within clades are driven by ecological and historical factors that differ among clades (Taylor and Gotelli 1994) and vary geographically (Gaston and Blackburn 1996).

The distinction between predominantly deterministic causes at one level and statistical pattern at a higher level is a recurring theme in evolutionary ecology and biogeography (May 1973; Sugihara 1980; Tokeshi 1990; Brown 1995; Maurer 1999; Hubbell 2001). To take a simple example, although human height is a complex but largely deterministic outcome of interaction between genes and environment, we are comfortable ignoring this complexity in expecting the relative frequencies of our body heights to follow a random normal distribution.

MDE models view the real-world distribution of species within a geographical domain as a statistical aggregate. They are phenomenological models of spatial pattern, regardless of what process the models themselves use to generate predictions (e.g., Grytnes, 2003*a*). The question that MDE analyses ask of an empirical data set is straightforward: to what degree do the biological, environmental, and historical processes that undeniably act on individual species and clades produce spatial patterns of richness that resemble those produced by the MDE model? To that degree, explanations arising from the response of species richness to domain gradients are potentially weakened. As discussed in "Multivariate Approaches," because richness patterns rarely prove to have single causes, only an appropriate multivariate analysis that incorporates all candidate explanations can yield a quantitative assessment of the relative contributions of MDE and other causes to an empirical pattern of richness.

Several authors (Hawkins and Diniz-Filho 2002; Laurie and Silander 2002; Zapata et al. 2003) have questioned whether it is legitimate that MDE models shuffle ranges geographically to predict patterns of richness. They argue that real ranges reflect dynamic interactions between species and environments, which would change if the species were moved somewhere else. Moreover, they suggest, because MDE models assume an absence of climatic gradients, every species "placed" in the domain by an MDE model must eventually spread to occupy the entire domain, yielding a constant richness throughout.

These authors appear to have missed the crucial distinction between the real-world dynamic processes that shape the geographical ranges of individual species and the statistical, spatial pattern that such ranges produce in the aggregate. It is the spatial pattern of range location that MDE models are concerned with, assuming realistic levels of range coherence. The shuffling of coherent ranges within domain limits is simply a resampling algorithm to estimate expected patterns under the assumption of random range location, not a claim that real species ranges are fixed entities. That climatic and historical gradients manifestly affect the evolution and ecology of individual species ranges in nature is not in question and is logically independent of patterns of range overlap. See appendix B ("An Analogy for Explaining MDE") for further development of this theme.

Related confusion of pattern with process appears to account for claims that MDE models assume that "speciation and extinction occur randomly over space" (Zapata et al. 2003, p. 682) and that "limits of species distributions and domain boundaries are stable through time" (Zapata et al. 2003, p. 683). Existing MDE models (with the exception of the evolutionary model of Bokma et al. 2001) need not assume anything about the spatial distribution of species origination or extinction in nature or about past or future temporal patterns; they assume only that range patterns, at a moment in time, are located as if placed at random. Accounting for the effects of geometric constraints using an appropriate MDE model is an effective means of pinpointing regions where a net excess or net deficiency of species remains (Rahbek 1997; Connolly et al. 2003; McCain 2004)—deviations that might be explained by spatial patterns of speciation and extinction. Likewise, MDE models offer a baseline for comparing paleopatterns of richness with contemporary patterns in light of changes in domain limits (e.g., the closing of the Isthmus of Panama, which joined two continents but separated two oceans). In terms of MDE theory, the expected result of such domain limit changes is a shift in the location of richness peaks.

The Role of Range Size Frequency Distributions

MDE model predictions depend crucially on the frequency distribution of range sizes (range size frequency distribution [RSFD]) from which "ranges" (line segments or polygon areas) are randomly sampled and randomly placed within the domain (Colwell and Hurtt 1994; Lees et al. 1999; Colwell and Lees 2000*a*; Koleff and Gaston 2001; Diniz-Filho et al. 2002; Laurie and Silander 2002; McCain 2003). Two otherwise identical MDE models with different RSFDs produce different patterns of richness when ranges are placed randomly on a domain (Colwell and Hurtt [1994] and Laurie and Silander [2002] provide theoretical examples, and Koleff and Gaston [2001] and McCain [2003] provide empirical ones). It is easy to see this intuitively by means of an extreme contrast. If each range in the RSFD is larger than half the size of the domain, they must all necessarily overlap in the middle of the domain. In this case, the mid-domain peak will be higher and broader than for an RSFD (with the same number of ranges) in which all ranges are less than half the size of the domain.

Table 1: Twenty-one Empirical Studies of the Mid-Domain Effect[a]

Reference	Location	Taxon	Gradient	1-D[b]	2-D[b]	Model	Multivariate?
Ellison 2002	Pacific basin	Mangroves	Lat.	78%		Midpoint resampling	No[c]
			Lat.	66%[c]		Range resampling	No[c]
Koleff and Gaston 2001	New World	Parrots	Lat.	51%		Fully stochastic[d]	No
		Parrots	Lat.	46%		Range resampling[e]	No
		Parrots	Lat.	96%		Midpoint resampling[f]	No
		Woodpeckers	Lat.	75%		Fully stochastic[d]	No
		Woodpeckers	Lat.	61%		Range resampling[e]	No
		Woodpeckers	Lat.	92%		Midpoint resampling[f]	No
Laurie and Silander 2002	Africa	Proteaceae	Lat.	23%		Fully stochastic	No
	Cape Region	Proteaceae	Lat.	30%		Fully stochastic	No
McCain 2003	N American deserts	Rodents	Lat.	88%, 93%[g]		Fully stochastic	Yes[g]
				Within 95% CI[g]		Range resampling	Yes[g]
				Within 95% CI[g]		Midpoint resampling	Yes[g]
Willig and Lyons 1998	New World	Bats	Lat.	67%, 71%, 77%[h]		Fully stochastic	No
	New World	Marsupials	Lat.	35%, 69%, 94%[h]		Fully stochastic	No
Connolly et al. 2003	Indo-Pacific	Corals	Lat.	Substantial[i]		Range resampling	Yes[j]
		Reef fishes	Long.	Substantial[i]		Range resampling	Yes[j]
		Corals	Lat.	Moderate[i]		Range resampling	Yes[j]
		Reef fishes	Long.	Moderate[i]		Range resampling	Yes[j]
Bokma et al. 2001	N America	Mammals	Lat.	Negative[k]		Evolutionary	No
	S America	Mammals	Lat.	66%[k]		Evolutionary	No
	New World	Mammals	Lat./long.	0%[k]		Evolutionary	No
Diniz-Filho et al. 2002	S America	Falconiformes	Lat./long.		0%[l]	Fully stochastic	No
		Strigiformes	Lat./long.		3%[l]	Fully stochastic	No
Hawkins and Diniz-Filho 2002	N America	Breeding birds	Lat./long.		21%[m]	Fully stochastic	No
Jetz and Rahbek 2001	Sub-Saharan Africa	Breeding birds	Lat.	66%		Spreading dye	No
			Long.	61%		Spreading dye	No
			Lat./long.		21%	Spreading dye	No
Jetz and Rahbek 2002	Sub-Saharan Africa	Breeding birds	Lat./long.		Significant[n]	Spreading dye	Yes[n]
Lees et al. 1999	Madagascar	Vertebrates, insects	Lat.	85%[o]		RSFD-adjusted, fully stochastic	Yes[p]
			Lat./elevation		75%[o]	RSFD-adjusted, fully stochastic	Yes[p]
Fleishman et al. 1998	Nevada	Butterflies	Elevation	Slight[q]		Range resampling	Yes[q]
Grytnes 2003*b*	Norway	Vascular plants	Elevation	Substantial[r]		Qualitative[r]	Yes[r]
Grytnes and Vetaas 2002	Himalayas (Nepal)	Vascular plants	Elevation	Moderate[s]		Max RS-adjusted, random optimum[s]	No
Kessler 2001	Bolivia	Acanthaceae	Elevation	0%[t]		Range-limited, fully stochastic[t]	Yes[t]

		Araceae	Elevation	18%[t]		Range-limited, fully stochastic[t]	Yes[t]
		Bromeliaceae (epi)[t]	Elevation	49%[t]		Range-limited, fully stochastic[t]	Yes[t]
		Bromeliaceae (terr)[t]	Elevation	7%[t]		Range-limited, fully stochastic[t]	Yes[t]
		Melastomataceae	Elevation	14%[t]		Range-limited, fully stochastic[t]	Yes[t]
		Palmae	Elevation	32%[t]		Range-limited, fully stochastic[t]	Yes[t]
		Pteridophyta (epi)[t]	Elevation	76%[t]		Range-limited, fully stochastic[t]	Yes[t]
		Pteridophyta (terr)[t]	Elevation	50%[t]		Range-limited, fully stochastic[t]	Yes[t]
McCain (2004)	Costa Rica	Nonvolant small mammals	Elevation	45%		Range resampling	Yes[u]
Rahbek 1997	S America	Birds	Elevation	Moderate[v]		Area-adjusted richness	No
Sanders 2002	Colorado	Ants	Elevation	13%		Range resampling	No[w]
	Nevada	Ants	Elevation	91%		Range resampling	No[w]
	Utah	Ants	Elevation	37%		Range resampling	No[w]
Pineda and Caswell 1998	NW Atlantic	Gastropods	Depth	Substantial[x]		Range resampling with rarefaction	No
		Polychaetes	Depth	Moderate[x]		Range resampling with rarefaction	No
Smith and Brown 2002	North Pacific	Pelagic fish	Depth	Nil[y]		Nested subset	No

[a] Studies are ordered first by gradient (latitude, then latitude/longitude or latitude/elevation, then elevation, then depth) and within categories alphabetically by author. Mora et al. (2003) might be considered an additional study, but the same data are more thoroughly analyzed in an MDE context by Connolly et al. (2003). Lat. = latitude; Long. = longitude

[b] Columns 1-D and 2-D present, for one-dimensional and two-dimensional models, respectively, the percentage variance explained by simple correlation of observed richness versus MDE predicted richness, unless otherwise noted.

[c] The range resampling result was computed by us from Ellison's (2002) original data. Midpoint resampling overestimates the effect of MDE. Neither result for mangroves has been corrected for area.

[d] Koleff and Gaston's (2001) model A is the fully stochastic model. Note that the r^2 for this model is higher than for the range resampling model, for both parrots and woodpeckers, counter to general expectations (and to the assertion of Zapata et al. [2003, p. 683] that the resampling model necessarily yields "an inflated probability of Type II error"). The explanation appears to be that the theoretical RSFD somewhat approximates the empirical RSFD, but the richness predictions for the theoretical RSFD happen to mimic some feature of the empirical richness curves that are caused by factors other than MDE—further evidence of the misleading results possible when theoretical RSFDs are assumed.

[e] Koleff and Gaston's (2001) model D is the range resampling model. See note d.

[f] Koleff and Gaston's (2001) Model E is the midpoint resampling model, which tends to overestimate the effect of MDE (see text).

[g] McCain (2003) tested all models with two alternate data sets: including and excluding Baja California peninsular endemics. For the fully stochastic model, these data sets yielded the first and second tabled r^2 values, respectively; the predicted curves were not coincident with the empirical curve, however, due to the inappropriate RSFD for this model, despite the high r^2 values. No r^2 value was reported for the resampling models, but the empirical curves lay well within the 95% confidence interval (CI) for the MDE predictions. Area, inadequate sampling, productivity, or failure to include nonendemics were not explanatory.

[h] Willig and Lyons (1998) give results for three domains (the three values for each taxon): continental limits, distributional limits, and 95% of distributional limits.

[i] Using the displacement statistic of Veech (2000) to assess deviation of observed richness from MDE predictions, Connolly et al. (2003) showed that the empirical patters for both latitude and longitude and for both corals and reef fishes differed significantly from MDE predictions; they focus on causes of deviation from MDE. Connolly et al. did not assess variance explained by MDE; the characterizations "substantial" and "moderate" are based on our visual assessment of their figure 2. Mora et al. (2003, p. 934) plot virtually the same data as Connolly et al. for fishes, randomize ranges and midpoints, and conclude that the patterns are "similar in shape" to MDE predictions but reject MDE as contributory because of significant deviations of empirical patterns from these predictions.

[j] Connolly et al. (2003) controlled for area orthogonal to latitude or longitude by conducting separate analyses on orthogonal "slices" of the two-dimensional distribution of corals and reef fishes. For example, to control for variation in longitudinal extent of the domain, they assessed richness patterns for latitude at several longitudes.

[k] The Bokma et al. (2001) study is listed with other two-dimensional studies because the percentages tabled here are based on correlations between latitudinal projections of their bimodal null model and corresponding segments of Willig and Lyons's (1998) empirical data. They report a correlation of $r = -.812$ ($r^2 = 0.66$) for North America. The statement by Hawkins and Diniz-Filho (2002) that the coefficient of determination is 8.5% for New World mammals in the Bokma et al. study is incorrect; the correct value is 0.000036%.

[l] In the Diniz-Filho et al. (2002) study, including nonendemic species changed the coefficient of determination from 0% to 5% for Falconiformes, from 3% to 2% for Strigiformes.

[m] For the widest-ranging quartile in the Hawkins and Diniz-Filho (2002), the coefficient of determination was 24%.

[n] In a six-predictor spatial linear model, MDE had a highly significant effect ($t = 6.42$, $P < .0001$), largely due to wide-ranging species, independent of habitat and climatic variables (of which the most significant was net primary productivity, with $t = 17.22$).

[o] Coefficients of determination are from Colwell and Lees (2000*a*), based on data of Lees et al. (1999).

[p] The results of Lees et al. (1999) were controlled for area and sampling effort. Correlations with environmental variables (rainfall, hydric credit, solar radiation, temperature, PET, biomass, respiration, carbon yields, and habitat diversity) were not explanatory in this study.

[q] Fleishman et al. (1998, p. 2489) rejected a fit to MDE predictions based on a Kolmogorov-Smirnov test but "concede that our species richness peak may be partially a product of nonbiological processes" (MDE) although "ecological processes play a significant role."

[r] Grytnes (2003*b*, p. 298) reports "indications in support of hard boundaries" (MDE) in four of seven transects, based on shape, symmetry, and elevation of the peak of empirical midelevation richness maxima, based on polynomial regressions. A fifth transect has an asymmetric richness hump, but the other two (at very high latitude) show monotonic declines in richness with elevation and thus a poor fit to qualitative MDE predictions. Grytnes finds no support for area, temperature, precipitation, or heterogeneity as important determinants of the mid-domain richness peaks in his data, but mass effect may play an important role.

[s] Grytnes and Vetaas (2002) did not quantify the fit of their MDE models to the empirical curves. In their models, an optimum (midpoint) is chosen first, from either a uniform or monotonic-decreasing distribution, then a range is selected from a uniform distribution bounded by the empirical maximum range size (max. RS). Unlike other MDE models, midpoints, but not complete ranges, must lie within the domain.

[t] Kessler (2001, following Colwell and Hurtt 1994) used the fully stochastic null model constrained by an upper range limit. Kessler set the maximum range to 3,200 m, the largest range size observed among all taxa tabled. terr = terrestrial; epi = epiphytic. Kessler analyzed several variables in univariate analyses but compares the results in his discussion. He compared MDE predictions to both plot richness and estimated habitat richness. Because the latter introduces an area effect, the values tabled here are plot richness.

[u] In addition to reporting r^2, McCain (2004, p. 19) generated 95% confidence intervals for the MDE predictions and reported that "most of the empirical curves of species richness occur within 95% prediction curves…although deviations from the model exist." Area was explicitly controlled; productivity and "community overlap" were not explanatory.

[v] Rahbek (1997) reported an asymmetric hump-shaped species richness pattern with elevation, with its peak below midelevation, when species richness was corrected for the area in each elevational band. No MDE model was statistically compared, but Rahbek argued that much of the pattern was most likely caused by geometric constraints.

[w] Values in the table for Sanders (2002) are not adjusted for area. For Colorado, including the area raises the coefficient of determination from 13% to 90%; for Nevada, from 91% to 99%; for Utah from 37% to 57%.

[x] Pineda and Caswell (1998) measured several aspects of correspondence between their (complex) MDE predictions and empirical data but did not report any overall value for correlation. Characterization of the degree of correspondence as substantial for gastropods and moderate for polychaetes is based on our visual assessment of their results in relation to other studies.

[y] Smith and Brown (2002) did not analyze any quantitative MDE predictions but (correctly) conclude that the fit would be negligible.

Theoretical Range Size Frequency Distributions

To explore the fundamental properties of MDE, the first MDE models (Colwell and Hurtt 1994; Willig and Lyons 1998) assumed theoretical RSFDs. The simplest graphical null model of the effect of geometric constraints in one dimension is a uniform random density of feasible coordinate pairs in a two-dimensional plot of range versus midpoint (Colwell and Hurtt's [1994] model 2, shown by Colwell and Lees [2000*a* in their fig. 1 and box 2] to be identical to both the analytical binomial model of Willig and Lyons [1998] and to MacArthur's [1957] overlapping niche model). This "fully stochastic model" (Colwell and Lees 2000*a*) produces a monotonically decreasing frequency of range sizes with a maximum range size equal to the full breadth of the domain and a particular distribution of range midpoints concentrated toward mid-domain. (The RSFD is defined by the cumulative ranked distribution function $d(r) = 2r - r^2$, where r is proportional range size and $0 < r < 1$.)

To show that the qualitative MDE is robust to the peaked distribution of range midpoints produced by the fully stochastic model, Colwell and Hurtt (1994) modeled MDE constrained to a uniform random midpoint distribution (for which Laurie and Silander [2002] derived the analytic form). Later, Colwell (2000) modeled MDE constrained to a uniform random range size distribution (for which Colwell and Lees [2000*a*] derived the analytic form). Colwell and Hurtt (1994) explored the effect of truncating the fully stochastic model at an upper limit of range size (implemented in an empirical study by Kessler [2001]).

Bokma et al. (2001) and Laurie and Silander (2002) extended the fully stochastic analytical model of Willig and Lyons (1998) to two dimensions. In rejecting this two-dimensional model as unsuitable, Laurie and Silander (2002) pointed out that the expected richness along transects across the rectangular domain depended on the direction of the transect; only transects parallel to an edge of the rectangle correspond to the one-dimensional analogue. In addition to this limitation, the two-dimensional fully stochastic model, like its one-dimensional analogue, presumably assumes a particular fixed RSFD (where range "size" means range area) with maximum range area equal to the entire domain, although neither an analytical formula nor a numerical approximation for the RSFD of this model has been derived.

Range Size Frequency Distributions in Empirical Assessments of MDE

Clearly, the choice of RSFD is critical in assessing the contribution of MDE to empirical patterns of richness. The objective of such assessments is to test whether MDE predictions differ from real-world patterns due to nonrandom location of ranges in the real world, not to test whether the empirical RSFD differs from a theoretical one. Yet if a particular, theoretical RSFD is used (or assumed) by a model in generating MDE predictions, differences between predictions of the model and the empirical richness pattern confound differences due to range placement (which we want to measure) with differences due to deviation of the theoretical RSFD from the empirical RSFD (which is not of interest for present purposes).

For this reason, we conclude that the empirical RSFD for the data to be assessed should be resampled to create predicted richness patterns. Moreover, using the empirical RSFD implicitly incorporates into the model taxon-specific biological characteristics that are logically independent of spatial patterns of richness within the domain. Among other things, vagility, body size, population density, and evolutionary potential for speciation and extinction in the context of a specific domain all interact to determine the empirical RSFD.

The most straightforward way to produce MDE model predictions using the empirical RSFD is to draw ranges at random from the empirical RSFD and place them randomly within the domain. In one dimension (for transect data, depth, elevation, latitude, etc.), model 4 of the computer application RangeModel (Colwell 2000) carries out the resampling (with replacement; see McCain, 2004) and exports the results. An analytical approach using empirical RSFDs is also available for one-dimensional data (Lees et al. 1999). For two-dimensional analyses, the "spreading dye" algorithm of Jetz and Rahbek (2001, 2002) resamples the empirical two-dimensional RSFD (range areas) and grows corresponding ranges in a grid by a nearest-neighbor rule, starting from random cells within a gridded domain of any shape. Many variations on the Jetz and Rahbek algorithm are possible and allow exploration of the effects of different model assumptions.

The process-based evolutionary model of Bokma et al. (2001; not to be confused with the Bokma fully stochastic model), which explicitly incorporates speciation, extinction, and migration, is an interesting alternative approach to generating two-dimensional MDE predictions. However, because it fails to constrain the simulated RSFD to match the corresponding empirical RSFD, Bokma et al.'s (2001) dynamic model suffers from the same problems as other models that assume a single theoretical RSFD for all taxa (although this shortcoming might be overcome in future evolutionary models).

On the face of it, using a purely theoretical RSFD might seem less subject to biological assumptions than using an empirical RSFD and therefore more truly "null," as argued by Koleff and Gaston (2001) and Laurie and Silander (2002). In fact, however, these theoretical models make the implicit biological assumptions that the range size distribution for all species, regardless of taxon or domain, is precisely the same and that the maximum species range covers the entire domain. The former assumption is clearly unrealistic (Anderson 1984; Brown 1995; Gaston 1996, 2003; Lees et al. 1999), and the latter is only sometimes correct, usually in relatively small domains (Lees et al. 1999; Gaston and Blackburn 2000; McCain 2003).

If an MDE model is based on an RSFD that differs substantially from the empirical RSFD, the observed species richness gradient cannot be reproduced by any spatial arrangement of the empirical ranges, random or otherwise. Therefore, comparing an empirical richness pattern with an expected richness pattern based on an unrealistic theoretical RSFD tends to underestimate the role of MDE because the predicted pattern is unobtainable. McCain (2003) gives an empirical demonstration of the effect of confounding differences due to range placement with differences due to deviation of the theoretical RSFD from the empirical RSFD. Hawkins and Diniz-Filho (2002) and Diniz-Filho et al. (2002) relied solely on the two-dimensional fully stochastic model, whereas Willig and Lyons (1998) and Laurie and Silander (2002) used the one-dimensional fully stochastic model to assess the role of MDE in empirical richness patterns, suggesting that the fit to MDE was probably underestimated in these studies. See "RSFDs and Model Choice in Assessing MDE" in appendix C for additional comments and critique.

One must also consider the possibility of overestimating the role of MDE. Does sampling from the empirical RSFD inevitably reproduce ("smuggle in") the spatial pattern of empirical species richness, as suggested by some authors (e.g., Zapata et al. 2003)? Actually, random samples from virtually any empirical RSFD, if placed on a domain according to nonrandom rules (e.g., a bias toward one side of the domain or toward opposite sides or focused nonrandomly in the middle), can produce a great variety of richness patterns that differ profoundly from MDE patterns based on the same RSFD (e.g., fig. 1 of Brown 2001). Moreover, the poor fit of MDE models for some empirical data sets is real-world evidence that MDE predictions need not reproduce the pattern of empirical richness (table 1). Examples include (for one dimension) the elevational richness patterns for Colorado ants (Sanders 2002) and Andean Acanthaceae (Kessler 2001), the distribution of richness with depth for Pacific Rim fishes (Smith and Brown 2002), the latitudinal distribution of African Proteaceae (Laurie and Silander 2002), and (in two dimensions) the richness patterns for South American birds of prey (Diniz-Filho et al. 2002). (The last four studies did not resample empirical ranges, but the empirical richness distributions would clearly deviate very substantially from any MDE model that resampled ranges.)

Zapata et al. (2003, p. 683) are correct that, compared to randomizing a theoretical RSFD, randomizing the empirical RSFD "will tend to predict a species richness peak similar in height to that observed" (assuming that the theoretical RSFD is a poor match for the empirical one). But rather than being a fault, we contend that this potential match is an important part of the design of the null model that nonetheless allows not only empirical curve shape but empirical curve height to differ substantially from the expected. In summary, contrary to the concern of Zapata et al. (2003, p. 683; see also Koleff and Gaston 2001) that randomizing the placement of empirical ranges produces "an inflated probability of Type II error," using any other distribution of range sizes instead inflates Type I error. (See footnote d in table 1 for further discussion of this issue.)

A related issue arises with MDE models that retain empirical range midpoints while randomly choosing feasible range sizes from a uniform range size distribution for each empirical midpoint. This model was introduced by Lyons and Willig (1997), implemented in Colwell (2000; model 5), and used by Ellison (2002) and (together with other models) by Koleff and Gaston (2001) and McCain (2003). Because the realized RSFD in such "midpoint" models may or may not correspond to the empirical RSFD, these models can suffer from the same Type I error problems as models that use theoretical RSFDs. On the other hand, when empirical richness patterns are substantially asymmetrical around the domain center, midpoint models tend to reproduce the empirical shape of the richness pattern, a source of Type II error (Koleff and Gaston 2001; Zapata et al. 2003). In short, because of these complex problems with inference, we believe that midpoint models should no longer be used for assessing the role of MDE for richness patterns. See "Biased Data Set Selection" in appendix C for further discussion on another form of bias.

Partitioning the RSFD: Range Size Categories and MDE

Geometric constraints are expected to affect the distribution of species with large ranges more than they affect species with small ranges (Colwell and Hurtt 1994; Pineda and Caswell 1998; Lees et al. 1999) because small-ranged species are free to occur (or not occur) virtually anywhere within a domain, whereas range centers of large-ranged species must cluster near mid-domain. Thus, MDE null models are expected to be better predictors for large-ranged than for small-ranged species. For the same reasons, groups of species or clades with small ranges (relative to the domain they occupy) are less likely to exhibit mid-domain peaks in richness consistent with MDE predictions. Both hypotheses are easily amenable to testing and have repeatedly been confirmed (see "Assessing MDE in Empirical Data Sets").

Defining Biotas, Ranges, and Domains

Range Continuity and Coherence

Using a sufficiently fine-scale spatial grid, no species has a continuous range, but at larger scales, ranges do appear increasingly continuous, in the sense of filling all cells of a grid between range boundaries. At any spatial scale, recorded occurrences of a species are more likely to be close together than far apart. Such positive spatial autocorrelation of incidence, or range coherence, is "an inherent quality of biogeographical data" (Rahbek and Graves 2000, p. 2262). Disjunct and patchy range distributions at scales of biogeographical interest do occur but are rare relative to continuous ranges. Moreover, patchiness in distributions compiled at regional scales often reflects undersampling rather than true range discontinuity (Grytnes and Vetaas 2002, Gaston 2003), and strikingly disjunct distributions often prove to represent distinct species on closer study. Hence the common assumption of range continuity between recorded limits in large-scale biogeographical studies is a simplification but rarely a source of significant bias for most taxa. There are exceptions, however, such as corals or reef fish (Connolly et al. 2003), for which actual "areas of occurrence" are widely dispersed within the "extent of occurrence" (in the terminology of Gaston and Blackburn 2000).

Patchiness in geographic distributions, when genuine, means that local richness tends to be overestimated by empirical range overlap counts as well as by MDE predictions. This does not seem to us to be a reason to dismiss studies that require this assumption, as Whittaker et al. (2001), Laurie and Silander (2002), and Zapata et al. (2003) have suggested. It simply means such studies are based on maximum richness estimates. Adding moderate "porosity" to ranges does not eliminate mid-domain peaks in MDE model predictions (N. J. Gotelli, unpublished analyses) any more than it would eliminate richness patterns in empirical maps. Zapata et al. (2003) point out that a set of ranges with zero coherence is equivalent to random dispersion of each species over the entire domain (which produces no MDE), but range coherence rarely if ever approaches zero in nature.

Endemic Species versus All Species

Most published MDE models have based the analysis solely on species restricted to the domain under study; in other words, species endemic to the domain (Colwell and Lees 2000*a*). This limitation has been pointed out as a potential weakness of existing MDE models (Koleff and Gaston 2001; Rahbek and Graves 2001; Whittaker et al. 2001; Hawkins and Diniz-Filho 2002; Laurie and Silander 2002). Ranges of nonendemic species overlap the boundary of the domain, by definition. For example, some taxa with range centers in northern South America extend into Central America and vice versa, thus overlapping the domain boundary if "South America" is defined as the domain (as in Diniz-Filho et al. 2002).

What is the effect of such nonendemics on MDE model predictions? Suppose the within-domain portion of each nonendemic's range was treated in the same way as endemic ranges in an MDE resampling model for South America. Then, after range resampling and random placement, the spatial pattern of species richness predicted by the model would be falsely concentrated toward the center of the domain, poorly matching the empirical pattern (of endemic plus nonendemics) and thus underestimating the role of MDE. An alternative algorithm would be to force the ranges of nonendemic species to abut the domain boundary in the resampling algorithm. However, this approach is open to the opposite criticism, that the model is overconstrained, thus overestimating the fit to the MDE model.

So the problem is complex, but it is not intrinsically insoluble. Grytnes and Vetaas (2002) explored the predictions of MDE models that incorporate nonendemic species by including the within-domain portion of all ranges for which the range midpoint occurs within the domain while excluding ranges for which the midpoint occurs outside the domain. A mid-domain peak nonetheless appears in the model, but richness does not drop to zero at the domain boundaries as it does in other MDE models. (Grytnes [2003*a*] considered further model variations that include source-sink, migration, and differential extinction of narrow-ranging species.) For empirical studies, a sensible approach, followed by Jetz and Rahbek (2001), Diniz-Filho et al. (2002), and McCain (2003), is to compare the results of analyses with and without endemic species included. In none of these three cases did it make much difference whether endemics were included. For South American birds, the fit to MDE predictions was very poor, with or without endemics (Diniz-Filho et al. 2002); for North American desert rodents, which show a latitudinal mid-domain peak statistically concordant with MDE model predictions, the empirical peak was simply lifted additively higher by including nonendemics (McCain 2003).

Even with restriction to endemic subsets of larger clades, evaluation of MDE can nevertheless provide insights and can usefully be evaluated in a multivariate context with climatic and other variables. For example, McCain (2003) showed that the previously undocumented mid-domain peak in the latitudinal pattern of species richness for rodents endemic to North American deserts (19°N to 45°N) was statistically concordant with MDE predictions (the empirical curve lies within the 95% confidence interval of MDE predictions from resampling empirical ranges) and cannot be explained by area (longitudinal width of the deserts), inadequate sampling, productivity, or failure to include nonendemics (despite the fact that the richness of all North American rodents increases steadily toward the south over the same latitudes).

Although most biogeographical studies traditionally focus on all representatives of a taxon in a region or continent (and there is certainly a continuing justification for such work), studies limited to endemics or studies that compare richness patterns of endemics to nonendemics (e.g., Vetaas and Grytnes 2002; McCain 2003) are legitimate in their own right and may well turn up interesting surprises. For example, Hawkins and Diniz-Filho (2002) discovered a clear mid-domain peak in the latitudinal (but not the longitudinal) distribution of North American endemic birds. (See "Endemic versus Nonendemic North American Birds" in app. C for further discussion.)

Setting Domain Limits

Another challenging issue is how to set the limits of the domain for computing MDE richness predictions. In introducing the idea of "hard" boundaries for domain limits, Colwell and Hurtt (1994) implied that domain limits should be boundaries that no species of the taxon under study can cross; for example, the land-sea interface for terrestrial mammals and marine fish. In contrast, "soft" boundaries are generally physiological domain limits, such as the northern and southern limits of mangrove distribution, both located at the winter seawater isotherms of about 20°C, where winter minimum air temperature remains above freezing (see Ellison 2002). Hard domain limits have often been viewed as nonbiological or physical and therefore more objective than physiologically defined soft domain limits (Koleff and Gaston 2001; Zapata et al. 2003). The distinction quickly breaks down on closer examination. In fact, domain limits for all MDE models are defined biologically by the limits of adaptation of the organisms. The reasons there are no whales in the Alps and no spruces in the Atlantic Ocean are just as biological, just as much a matter of adaptation, as the reasons there are no palms in the Alps and no spruces in the Sahara.

In principle then, we see no reason not to define biologically based domain limits on adaptations that are more subtle but just as critical as vertebrate lungs and fish gills, such as frost tolerance limits in plants, heat tolerance limits in animals, or terrestrial biome boundaries for species unable or unlikely to cross them. For example, Lees et al. (1999) defined the rainforest belt in Madagascar as the domain for their study of rainforest fauna, McCain (2003) defined the limits of her rodent study by the limits of the desert biome, Jetz and Rahbek (2001, 2002) restricted their analyses to the distribution of birds in sub-Saharan Africa, and Laurie and Silander (2002) focused on the Cape Floristic Province. Many other bioregions and biogeographical units would be excellent candidates as domains for MDE studies; for example, the Atlantic rainforest of Brazil, the Australian tropical rainforest of Queensland, and North American prairies or other relatively isolated grasslands.

The concept of the domain of a clade of species rests on the assumption that the clade collectively displays the evolutionary potential for occupying all points in the domain at some specified period in evolutionary time despite the fact that individual species within the clade are commonly unable to survive and reproduce at every point within the domain. The domain of a group of species defined in this way is a statistically emergent concept at a higher taxonomic level. The concept is actually a very old one. When biogeographers characterize a taxon as "restricted" to a certain region (or realm, or continent), they do not for a moment suppose that every species of the taxon could thrive in every part of the region.

For some taxa, the reasons for range limits are well understood (e.g., Terborgh 1973; Means and Simberloff 1987; Root 1988; Castro 1989; Ellison 2002; Gaston 2003). In the absence of such specific knowledge, the best guess regarding domain limits is simply the collective limits of distribution for the group, a sort of biological assay of the minimum domain. Willig and Lyons (1998) introduced this approach in defining the collective latitudinal range of New World marsupials and bats, and Koleff and Gaston (2001) followed the same procedure for New World parrots and woodpeckers. There is no a priori reason to expect this approach to produce a mid-domain peak if environmental or historical gradients strongly determine a different pattern of richness within such a domain. (Smith and Brown [2002] document just such a case.) Indeed, carrying out nested analyses for successively more inclusive taxa (therefore, in most cases, for successively larger geographical scales) might help reveal the spatial scale at which random versus deterministic (e.g., climatic) forces are most important. The null expectation for such an analysis would be a shift in the location of a mid-domain richness peak as the geographic scope is broadened to successively more inclusive taxonomic levels.

A domain defined from actual distributional limits tends to produce MDE predictions that agree more closely with observed richness patterns than MDE predictions based on a larger domain, since the endpoints or edges of the actual and predicted distribution necessarily coincide (Willig and Lyons 1998). Whether this tendency inflates Type

II error as Zapata et al. (2003) suggest depends on whether the hypothesis is conditioned on defining the domain by distributional limits. If we hypothesize that the observed pattern of richness, within the limits of distribution, does not differ from the pattern predicted by random placement of empirical ranges within those limits, there is no reason to expect any inflation of Type II error.

Koleff and Gaston (2001) point out that, as the number of species in the analysis approaches small numbers, the geometric "degrees of freedom" may become too small for meaningful randomization. However, even groups with as few as 20 species can still produce meaningful results in MDE model analyses (N. J. Gotelli, C. Rahbek, G. R. Graves, and R. K. Colwell, unpublished analyses). An evaluation of the spread of the sampling distribution produced by many runs of an MDE resampling model might be one way to evaluate this issue.

Assessing MDE in Empirical Data Sets

In this section, we summarize the results of all 21 published studies known to us (including a search of citation databases) that have investigated the role of MDE in shaping empirical patterns of species richness. The studies are tabulated and characterized in table 1 and summarized in

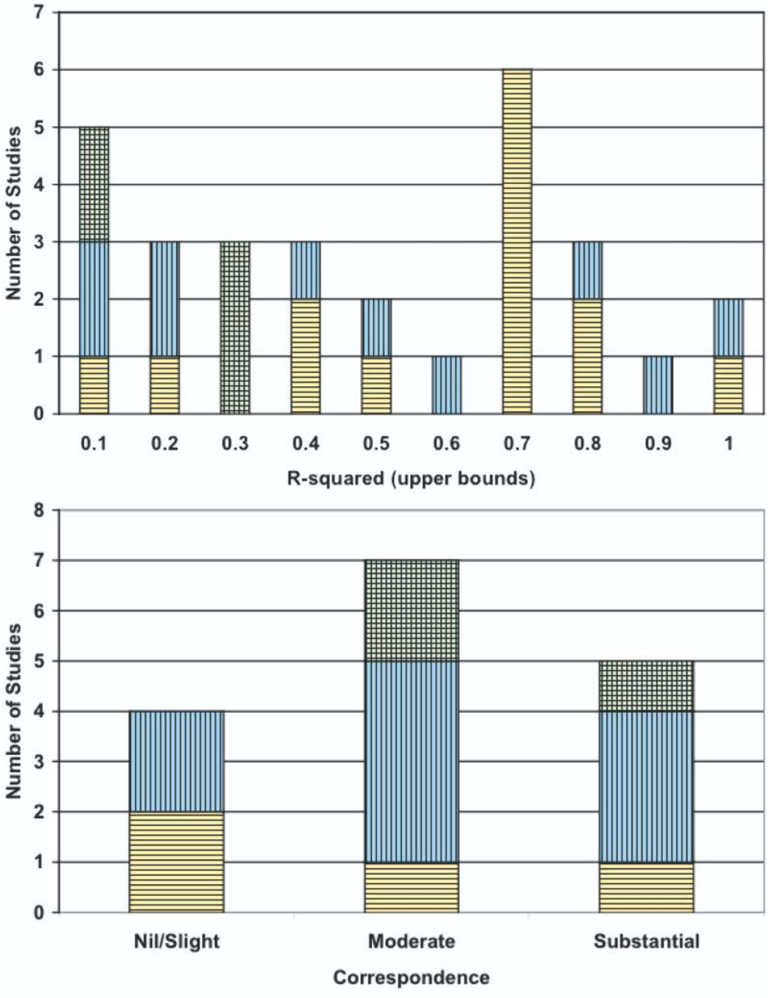

Figure 1: Assessment of mid-domain effect (MDE) in empirical studies. Summarizing the information in table 1, the upper graph displays results from all studies that reported coefficients of determination, whereas the lower graph attempts to represent the results of other studies that did not. *Horizontal hatching, yellow background*: one-dimensional studies, MDE only; *vertical hatching, blue background*: one-dimensional studies, multivariate; *cross-hatching, green background*: two-dimensional studies. When results for both fully stochastic and range-resampling models were reported for the same data set, the latter are plotted (even if less significant; see footnote d in table 1). No midpoint resampling results are included. For studies that examined the same data set from both one- and two-dimensional perspectives, both results are included in the graphs.

figure 1. (Zapata et al. [2003] provide a somewhat similar table for a subset of these studies.)

The papers summarized in table 1 are quite recent (more than half were published since 2002). Simulation, modeling, and statistical techniques for investigating MDE are still in their infancy but are actively being developed and debated. These studies have prompted a closer look at the influence of the size, location, and overlap of species ranges in geographical patterns. In classic null model fashion, some authors have effectively used the residuals from an MDE model to focus on the very environmental and historical gradients that MDE null models intentionally exclude (Jetz and Rahbek 2002; Connolly et al. 2003). Moreover, these studies show that MDE itself is likely to prove an important factor in many patterns of species richness, contrary to the conclusions of authors (e.g., Hawkins and Diniz-Filho 2002; Zapata et al. 2003) who have assessed many of the same studies from the "all-or-nothing" point of view that we discuss in "All or Nothing? Evaluating the Relative Importance of MDE."

Results from the empirical studies vary widely depending on domain, taxon, and method. As predicted by MDE theory, where ranges are small relative to the extent of the domain, MDE tends to be weaker (e.g., Laurie and Silander's 2002 study of Proteaceae with Africa as the domain); where many ranges are larger relative to the domain, MDE tends to be stronger (e.g., Lees et al.'s 1999 study of Madagascan species or McCain's 2003 study of North American desert rodents).

Likewise, studies that have partitioned ranges into range-size categories within the same data set (Pineda and Caswell 1998; Lees et al. 1999; Hawkins and Diniz-Filho 2002; Jetz and Rahbek 2002; Vetaas and Grytnes 2002) have universally found stronger support for MDE among large-ranged species rather than among small-ranged species, as predicted by MDE theory. More interesting biologically, Lees et al. (1999) and Jetz and Rahbek (2002) found that focusing on small-ranged species revealed important environmental effects for which little influence could be detected on large-ranged species, which are more constrained by geometry. As so often happens in science, this unexpected finding arose as a side effect of a different quest (assessing MDE), just as the discovery of MDE arose from considering ways to investigate Rapoport's rule (Colwell and Hurtt 1994; Rahbek 1997; Pineda and Caswell 1998; Willig and Lyons 1998).

Dimensionality

To date, 16 studies (covering 22 groups on 19 gradients) have used exclusively one-dimensional MDE models to study richness patterns for latitude, longitude, elevation, depth, or two gradients jointly (latitude and longitude or latitude and elevation); three studies have used exclusively two-dimensional models; and two studies have used both (table 1). No three-dimensional models (explicitly including elevation or depth as well as horizontal dimensions) have yet been published.

Some critics dismiss results of one-dimensional studies as of little or no interest because the world is not one-dimensional (Bokma et al. 2001; Diniz-Filho et al. 2002; Hawkins and Diniz-Filho 2002). Others argue that one-dimensional models are flawed by an "artificial reduction in dimensionality" that exaggerates MDE (Zapata et al. 2003, p. 684). These arguments do not hold up under scrutiny. Of course, the world is not two-dimensional either, yet biogeographers have productively studied two-dimensional patterns (flat maps) as well as one-dimensional (transects, gradients) and three-dimensional (topographic) patterns throughout the history of the field. Moreover, reduction in dimensionality is a common strategy (often even an objective) for studying complex patterns in science and statistics. By reducing dimensions, we simplify patterns at the expense of detail (e.g., univariate projections or the extraction of principal axes from multivariate data sets). The number of publications on one-dimensional perspectives on richness gradients is enormous. Must we suddenly no longer be interested in these patterns because they are "artificial"?

The most famous pattern of all is of course the latitudinal gradient of species richness (by definition a one-dimensional pattern), and a great deal of effort has been expended exploring the effects of other physical dimensions (area, topography) on this pattern (Rosenzweig 1995; Rohde 1997). One-dimensional MDE models of latitudinal distributions follow in this tradition. Other kinds of transects, including elevation, depth, and perhaps others are inherently one-dimensional. For highly fragmented two-dimensional distributions such as coral reef faunas in the Indo-Pacific (Connolly et al. 2003), working with two one-dimensional models orthogonally is actually more informative than a two-dimensional model that assumes a continuous distribution within range boundaries

Where feasible, presenting both one- and two-dimensional analyses of the same data set, either explicitly (Lees et al. 1999; Jetz and Rahbek 2001) or implicitly (Connolly et al. 2003), seems the strongest approach. Table 1 shows that, for the two studies that compared the fit of MDE models to the same (two-dimensional) data sets using both one- and two-dimensional models and analyses (Lees et al. 1999; Jetz and Rahbek 2001), the fit to two-dimensional models was weaker. Given that information on dimensional covariation is inherently absent in one-dimensional projections, this is to be expected. The three studies that used exclusively two-dimensional models (Bokma et al. 2001; Diniz-Filho et al. 2002; Hawkins and Diniz-Filho

2002) report low values (even one negative correlation) for variance explained by MDE. However, the MDE models used in all three of these used inappropriate RSFDs, and a reanalysis of biome-based subdomains might show a greater role for MDE in at least two cases, as explained in appendix C.

Multivariate Approaches

Fewer than half the studies in table 1 (eight of 21) considered candidate explanations for species richness patterns in addition to MDE, including area, topography, climatic, or historical correlates. (The last column in the table, with details in the table footnotes, indicates this information for each study.) The other 13 studies are best viewed as exploring the potential role of MDE in the empirical patterns; how well the results for these 13 studies will stand up in a multivariate comparison with other candidate explanations for species richness remains to be seen. The few multivariate results published so far that quantitatively assess a full range of factors (Lees et al. [1999] for Madagascan vertebrates and insects, Jetz and Rahbek [2002] for African birds, Kessler [2001] for certain Andean plants, McCain [2003] for North American desert rodents, and McCain [2004] for South American small mammals) collectively reveal a substantial contribution of MDE to the species richness patterns studied.

Accounting for map area (although not for surface area) is handled intrinsically in properly parameterized two-dimensional models, but in one-dimensional models, variation in domain area orthogonal to the MDE dimension must be explicitly controlled. This is not a new issue (Rosenzweig 1995; Rahbek 1997; Rohde 1997). For example, to create an area-corrected latitudinal data set from gridded map data is straightforward: simply compute mean "cell richness" for east-west longitudinal bands, each spanning, say, 5° of latitude. But the mean must be a cell-by-cell mean; dividing east-west "band sums" (the total richness within a longitudinal band) by corresponding band areas introduces biases (Jetz and Rahbek 2001) because richness is not a linear function of area (McCoy and Connor 1980; Gotelli and Colwell 2001). Thus Rahbek (1997) corrected for area in an elevational data set by estimating avian richness from elevation-specific species-area curves, instead of computing true cell means. McCain (2004) explicitly controlled for area in her sampling design. Connolly et al. (2003) controlled for area orthogonal to latitude or longitude by conducting separate analyses on orthogonal "slices" of the two-dimensional distribution of Indo-Pacific corals and reef fishes (see McCoy and Connor [1980] for a similar approach to accounting for area).

Statistical Issues

To assess the fit of an MDE model, many studies have computed the coefficient of determination (or correlation coefficient) between empirical species richness and MDE predictions at each sampling point on a gradient or in each grid cell of a map (table 1). There are two problems with this approach. First, with the exception of Jetz and Rahbek (2002), none of the studies we surveyed explicitly controlled for spatial autocorrelation. Failure to do so inflates sample size, thus increasing the chance of finding significant differences between MDE predictions and empirical data when in fact the differences are not significant (Cressie 1991; Zapata et al. 2003). New developments in the analysis of spatial autocorrelation in ecological data sets may provide tools for dealing with this problem in species richness studies (Ver Hoef et al. 2001; Liebhold and Gurevitch 2002).

Second, computing correlation coefficients (or coefficients of determination) to assess the fit of an MDE model requires a clear understanding of their limitations (Laurie and Silander 2002; McCain 2003; Zapata et al. 2003). The correlation coefficient reflects the fit of the data to the MDE predictions in terms of relative, not absolute, magnitude. Whereas substantial differences in curve shape yield low correlations, two identically shaped curves, displaced on the ordinate, yield perfect correlations. (McCain [2003] provides an empirical example in which MDE curve shapes are similar but absolute magnitude differs.)

An alternative approach is to examine the slope and intercept of the relationship between predicted and empirical richness. Only if empirical and MDE-predicted species richness are identical will the regression of observed on predicted richness have a slope of unity, with an intercept of zero. (Jetz and Rahbek [2001, 2002] used this approach.) Unfortunately, climatic variables cannot be tested with this approach because predictor variables such as potential evapotranspiration (PET) are not in units of species—an issue discussed in the next section.

Other approaches assess the fit of MDE by comparing empirical patterns to ad hoc sampling distributions based on range resampling. Pineda and Caswell (1998) computed polynomial regressions based on randomized range placements and then compared the distribution of curve parameters with those of a similar regression on the empirical data. Veech (2000) proposed a whole-curve deviation statistic for overall curve fit (used by Connolly et al. [2003]). McCain (2003, 2004) examined the location of the empirical richness pattern in relation to 95% confidence contours for predicted richness, based on resampling. Although these methods avoid the limitations of simple correlation coefficients (and coefficients of determination), they were designed for hypothesis testing rather than estimation of effect.

Also in a hypothesis-testing mode, two different approaches have been proposed to examine the "fine structure" of MDE predictions in relation to empirical data sets. Koleff and Gaston (2001) compared predicted and observed distributions for a number of β-diversity (turnover) measures for New World parrots and woodpeckers. In a study of South African Proteaceae, Laurie and Silander (2002) compared the spatial distribution of range/midpoint coordinate pairs with a uniform distribution of feasible points (the fully stochastic model) in a range/midpoint plot—an indirect way of examining turnover. In both cases, significant differences were found. Although MDE models might form a reasonable starting point for modeling species turnover, they were intended to model aggregate spatial patterns of richness, not the details of species turnover. Patterns of turnover do not map 1 : 1 with patterns of species richness because narrow-ranging species differentially affect measures of turnover, whereas wide-ranging species differentially affect spatial patterns of species richness.

All or Nothing? Evaluating the Relative Importance of MDE

Leaving behind a history of single-factor explanations for the major geographical patterns of species richness, the consensus view of most biogeographers and ecologists today is that multiple factors are surely at work and that any particular factor may be more or less important for different taxa, different places, and different spatial and temporal scales (Lawton 1996; Brown and Lomolino 1998; Gaston and Blackburn 2000; Rahbek and Graves 2000, 2001; Whittaker et al. 2001; Diniz-Filho et al. 2002; Jetz and Rahbek 2002; Connolly et al. 2003; Grytnes 2003*b*). MDE models have challenged biogeographers to consider the influence of geometric constraints and to use explicit null models as an analytical tool. However, it was never the claim of MDE theorists (Colwell and Hurtt 1994; Pineda and Caswell 1998; Willig and Lyons 1998; Colwell and Lees 2000*a*, 2000*b*; Jetz and Rahbek 2001) that geometric constraints were likely to explain all details of every pattern of richness any more than energy, temperature, PET, topography, precipitation, or isolation from source areas, individually, is likely to explain every pattern of richness at every spatial scale. The studies in table 1 and figure 1 show that MDE varies from remarkably explanatory in some cases (Lees et al. 1999; McCain 2003) to completely unimportant in others (Smith and Brown 2002).

MDE predictions should be evaluated statistically on an equal footing with other candidate explanations that accord equally well with empirical patterns. We do not agree with Bokma et al. (2001, p. 48) that "if random processes are able to predict a pattern then randomness enjoys priority over other explanations." Certainly in a statistical sense, there is no justification for treating MDE predictions as primary just because they are generated by a null model. While it might be tempting to claim that geometry is somehow more fundamental than other causes, solar energy, precipitation, and history are no less inevitable.

Given this pluralistic perspective, we disagree with the conclusion of Hawkins and Diniz-Filho (2002), Koleff and Gaston (2001), Laurie and Silander (2002), and Zapata et al. (2003) that, if MDE does not account for virtually all of a geographical pattern of richness, then it must be rejected as nonexplanatory. (As Zapata et al. [2003, p. 677] put it, "the models do not adequately describe observed species richness gradients and thus fail to explain them.")

In part, the all-or-nothing point of view may arise from confusion between null models and null hypotheses. MDE models predict species richness patterns under geometric constraints by intentionally excluding any effects of gradients on patterns of species richness. This makes them null models, but it is shortsighted to treat them strictly as null hypotheses to be rejected or accepted. MDE models specify the species richness patterns that would be expected from random range placement. The degree of concordance between these expected richness patterns and their empirical counterparts is a measure of the effect size of geometric constraints, preferably evaluated as one of several potentially contributory factors in a multivariate context.

Another reason that an all-or-nothing criterion tends to be applied to MDE models is that, unlike other candidate explanations for patterns of species richness, MDE models actually predict species richness itself, not as the dependent variable of a regression or other statistical model but as species counts in map units, in exactly the same form as empirical richness. In contrast, temperature, PET, productivity, topographic relief, and other such predictors do not by themselves generate direct predictions of species richness (but see Allen et al. [2002] for a kinetic model that does make quantitative predictions based on temperature). Instead, biogeographers have inferred the conditional importance of these variables through their correlations with species richness (numerous authors) or have used statistical models developed in one geographical area to make statistical predictions about richness elsewhere (Adams and Woodward 1989; Francis and Currie 1998; O'Brien 1998; see also Currie et al. 1999 for discussion).

Thus if a simple null hypothesis test of an MDE model is rejected at $P < .05$ (Pineda and Caswell 1998; Connolly et al. 2003; and implicitly, Mora et al. 2003), but observed species richness and MDE predictions are nonetheless significantly but imperfectly correlated (many studies in table 1), should MDE be "rejected" and declared nonexplanatory? In contrast, on what grounds do we reject gradient factors such as temperature or PET? We do so by showing they are not significantly correlated with richness or that they explain only a small percentage of the variation in species richness. By this criterion, MDE contributes substantially to observed variation in species richness in many of the one- and two-dimensional analyses listed in table 1.

In the short term, gradient models and MDE can be evaluated on the same footing by treating MDE as a candidate explanatory variable in spatial linear models that include other candidate factors (taking account of spatial autocorrelation; Ver Hoef et al. 2001 provide an introduction; Jetz and Rahbek 2002 provide an example of implementation). The long-term resolution is to develop mechanistic models that predict species richness for gradient-based hypotheses, perhaps based on aggregating species-level models of range evolution and ecology (Kirkpatrick and Barton 1997; Case and Taper 2000). Such models would force an explicit consideration of how spatial gradients in resources differentially affect the probability of colonization, persistence, and coexistence of species. We view this objective as an important challenge at the meso-scale interface between evolutionary ecology and biogeography.

Because controlled, manipulative experiments in macroscale biogeography are not feasible (even if they were ethical), factorial designs intended to assess the role of multiple explanations for richness patterns are limited to what nature happens to have produced. When many candidate factors are spatially correlated, statistical discrimination among them is difficult. For example, a flat domain centered on the Equator would be a daunting place to discriminate the relative importance of MDE, solar energy, mean annual temperature, and precipitation. But there are domains where MDE predictions contradict, or at least differ from, the predictions of climatic factors. These include domains that do not cross the equator (Madagascar, Lees et al. 1999; North America, Hawkins and Diniz-Filho 2002; North American deserts, McCain 2003); elevational gradients, for which no consensus climatic explanation exists for mid-domain peaks (Rahbek 1995, 1997; Kessler 2001; Grytnes and Vetaas 2002; Sanders 2002; Grytnes 2003*b*; McCain 2003, 2004); depth gradients (Pineda and Caswell 1998; Smith and Brown 2002); peninsular gradients (McCain 2003); longitudinal patterns (Jetz and Rahbek 2001; Connolly et al. 2003; Mora et al. 2003), and no doubt other puzzling richness gradients that remain to be explored in a multivariate context that includes MDE. Finally, outside the realm of biogeography, MDE models seem likely to prove useful in understanding other bounded, multispecies distributions, including microspatial, stratigraphic, gradient-response, intermediate disturbance, and phenological patterns.

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APPENDIX A

MDE and the History of Null Models

We were struck by the similarity between the emerging debate over MDE models and the earlier debate over null models in the early 1980s, and several reviewers also commented on parallels. The extensive history of null models in ecology has already been well documented (Harvey et al. 1983; Gotelli and Graves 1996; Weiher and Keddy 1999) and will not be repeated here. Instead we will emphasize the broad areas of congruence with the debate over MDE.

Misunderstanding the Underlying Nature of a Null Model. Many early critics of null models in ecology complained that ecological null models were void of mechanism and portrayed the world as having no structure or being entirely random (Roughgarden 1983). In fact, null models often incorporate considerable structure from the existing data (Gotelli 2000). The hypothesis for null models of community structure is not that communities are entirely random but that the occurrence of species is random with respect to one another (Strong 1980).

Similarly, MDE critics have complained that MDE models imply that species can occur anywhere within the domain. However, the correct statement is that MDE models depict species range boundaries as randomly placed with respect to climatic (or other) gradients.

Implicit Acceptance of an Incorrect Null Hypothesis. Early biogeographic studies used taxonomic diversity indices, such as the species/genus ratio, as an indicator of the severity of interspecific competition; competition was thought to reduce the number of species in a genus (or higher taxon) that could coexist (Järvinen 1982). The implicit null hypothesis was that, with random sampling, the expected ratios would be the same in both large and small communities (Elton 1946). But the species/genus ratio, like all taxonomic indices, changes dramatically with sample size and cannot be evaluated without reference to a statistical sampling model (Gotelli and Colwell 2001).

Similarly, much of the literature on effects of biotic and abiotic gradients on species richness implicitly assumes that the occurrences of a species can be entirely discontinuous across a domain. If this is true, then the null expectation is a flat diversity curve across the domain. However, if we accept that there is at least some continuity in species occurrences within the geographic range ("range cohesion" in our terminology), the proper null expectation is a hump-shaped diversity curve. MDE models attempt to account for this sampling effect of continuous geographic ranges, which is ignored by regression models that are fit to geographic gradients.

Early Use of Null Models with Poor Statistical Properties. In the analysis of binary presence-absence matrices, Gilpin and Diamond (1982) adapted a contingency table model that was analytically convenient to assess the statistical significance of species co-occurrence patterns. However, that model was analytically flawed (Gotelli and Graves 1996) and had undesirable Type I error properties so that the null hypothesis was often rejected, even with purely random data sets (Wilson 1987).

Similarly, some early MDE models (Colwell and Hurtt 1994; Willig and Lyons 1998) used theoretical range size frequency distributions, which are analytically convenient. However, as discussed in the main text, these distributions can cause the MDE model to be spuriously rejected. Computer-intensive models (e.g., Jetz and Rahbek 2002) that explicitly simulate the spread of a species geographic range preserve the observed RSFD and are less prone to the statistical problems of simpler models that rely on theoretical RSFDs.

Intellectual Resistance to Null Models That Challenge Widely Accepted Conventional Wisdom. The MacArthurian paradigm in ecology was that the behavior, morphology, population dynamics, species occurrences, and community structure of natural assemblages reflected the struggle for limited resources and the subsequent partitioning of the ecological niche (Wiens 1989). This widely accepted view dominated ecological research in the 1960s and 1970s. Much of the resistance to the use of null models came from the fact that such analyses called into question the ubiquity and influence of interspecific competition and indicated that communities might look much the same as they do even in the absence of strong species interactions (Gotelli 1999).

In the extensive literature on geographic gradients, there is no consensus on any single accepted mechanism to account for all observed gradients in species richness (Rohde 1992). Nevertheless, there seems to be widespread agreement that some direct or indirect mix of biotic, abiotic, and historical mechanisms must account for these patterns. MDE models challenge this accepted wisdom by suggesting that species richness gradients could also be attributed in varying degrees to the random placement of contiguous geographic ranges within a bounded domain. The growing body of evidence in favor of this hypothesis (table 1) undercuts misguided claims that MDE must be discarded as a causal factor for richness gradients.

The Future. Can we predict the future from the past? If the MDE debate follows the pattern seen in the null models controversy of the 1980s, then we can expect that the initial disputes over MDE models will not be cleanly resolved. However, a second generation of researchers will adopt MDE and/or other null models and employ them as useful tools in biogeographic analyses. Statistical advances will lead to increasingly sophisticated computer simulations that will address many of the criticisms of the early models. Finally, the increasing availability of dedicated software packages (Colwell 2000; Jetz and Rahbek 2001; Gotelli and Entsminger 2002) will allow researchers to explore MDE models with their own data sets and draw their own conclusions. Perhaps this time around these changes will take place more quickly, over a time span of years rather than decades.

APPENDIX B

An Analogy for Explaining MDE

We have found that a basic grasp of MDE models is prerequisite to understanding how MDE might shape richness patterns in nature. Many people understand physical models better than graphical or mathematical ones. In one dimension, the mid-domain effect could be called the "pencil box effect." Imagine a schoolchild's pencil box, about 1.5 times as long as a new writing pencil and 3 or 4 cm wide. The box contains a collection of pencils, some new, some older and shorter, and some mere nubbins just long enough to use. Shuffle the pencils (randomly) inside the box by shaking it back and forth, end to end. Now fill the pencil box with a hardening resin to fix the pencils in place, saw it up into 11 cross-sectional slices (like slicing a banana), and count the number of pencil cross sections

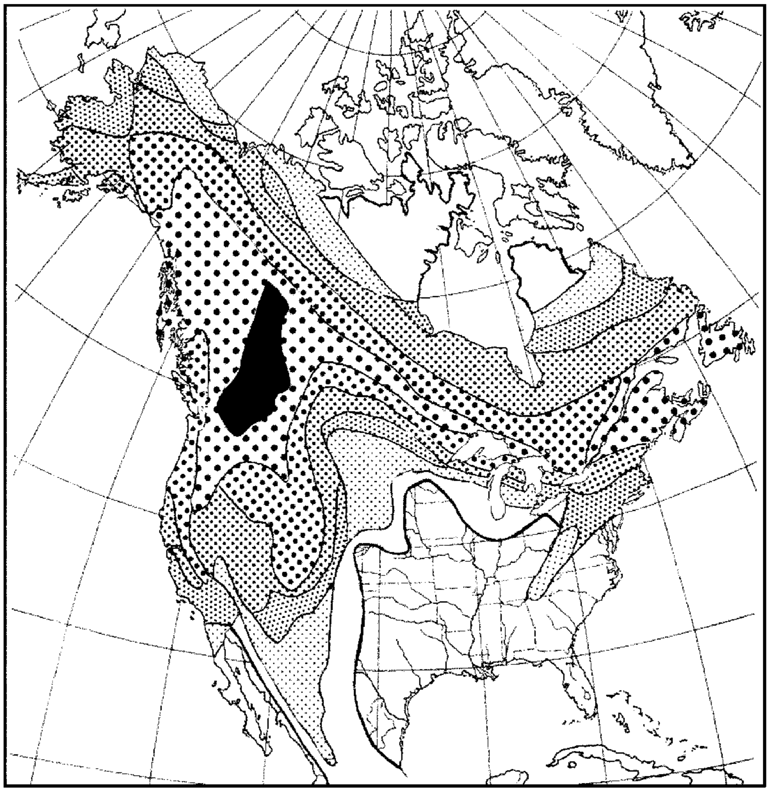

Figure C1: Species richness of North American birds endemic to montane forest-taiga; figure from Mengel (1970)

in each slice. Illustrating the mid-domain effect, the middle slice (the sixth) will contain the most, with the five slices progressively closer to each end of the box having fewer and fewer pencil bits.

Now imagine an elevational gradient, from sea level to the top of a mountain range (the pencil box), with a corresponding climatic gradient. Rigorously census the plant assemblage at each of 11 evenly spaced sites. Plants near sea level are well adapted to warmer lowland climates, those near the top of the range to colder climates of the highlands, and plants in the middle to their intermediate climate, but species (pencils) vary in how narrowly they are confined by climate (pencil length varies). Suppose the highest richness occurs at the sixth (middle) site, where we find a mixture of species—some that also occur in the lowlands, some that also occur in the highlands, and some found only at midelevations—with lower richness at lower and higher sites. This is exactly what we would expect if the mid-domain effect were responsible for the pattern of richness, assuming the real pattern of richness is closely matched by the mean of many random shuffles of the real ranges.

But, replies the skeptic, if climate is responsible for limiting each of these species to a certain range of elevations, is climate not then responsible for the midelevation peak? Perhaps, but not for that reason. The largely deterministic processes of adaptation, dispersal, and coexistence of many individual species may produce geographical patterns that have a nondeterministic (stochastic) explanation. Unless some environmental variable or combination of variables can be shown to fully predict the midelevation richness peak on our imaginary mountain range and similar peaks on other mountain ranges, MDE would emerge as a contributory explanation, or even suffice as the best explanation, whether that is satisfying to our biological curiosity and intuition or not.

APPENDIX C

Additional Critiques

RSFDs and Model Choice in Assessing MDE: Hawkins and Diniz-Filho and Laurie and Silander. Although their article makes clear that they were aware of the importance of the RSFD in shaping MDE predictions, Laurie and Silander (2002) elected to use the one-dimensional, fully stochastic

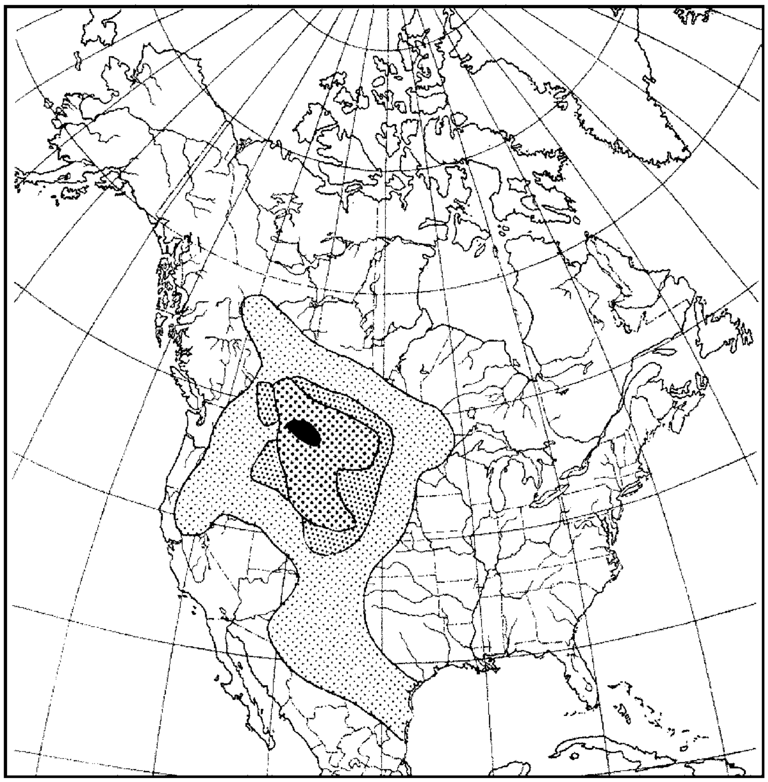

Figure C2: Species richness of North American birds endemic to grasslandsl; figure from Mengel (1970)

model to assess the role of MDE for African Proteaceae. Likewise, Hawkins and Diniz-Filho (2002) and Diniz-Filho et al. (2002) used the two-dimensional fully stochastic model to assess the role of MDE in empirical richness patterns for New World birds, despite the fact that the model assumes a rectangular domain and produces an unrealistic RSFD. Hawkins and Diniz-Filho (2002, p. 420) acknowledged that they were aware of the "critical underlying assumptions" of using a theoretical RSFD, and Diniz-Filho et al. (2002, p. 48) state that "other models based on randomization of geographical ranges or latitudinal extents across continent are available today and permit a clearer evaluation of their assumptions."

Tools that randomize empirical RSFDs were available (Colwell 2000; Jetz and Rahbek 2001). Why, then, did these authors use the fully stochastic models? Laurie and Silander (2002) did so on principle. They argued that only the fully stochastic model is truly "null" because all other models admit biological parameters. This argument suggests a misunderstanding of the nature of null models in ecology, as explained in the body of this article. Hawkins and Diniz-Filho (2002, p. 420) used the fully stochastic model "because of its computational simplicity and ease of interpretation." However, problems arising from applying the fully stochastic model to a two-dimensional domain with irregular domain boundaries required Hawkins and Diniz-Filho (2002) to make ad hoc adjustments that (judging from their fig. 1) solved a problem with peninsulas at the cost of creating an opposite problem with the Great Lakes. Diniz-Filho et al. (2002, p. 48) selected the fully stochastic, two-dimensional model for its "computational simplicity" but were later forced to reduce sample size from 780 quadrats to 32 because of "computational difficulties."

Endemic versus Nonendemic North American Birds: Hawkins and Diniz-Filho. Hawkins and Diniz-Filho (2002) studied birds whose breeding range is restricted to North America (endemics, in this sense) south to central Mexico, noting that this domain represents a traditionally recognized biogeographic region. The full avifauna of this region, however, includes a quite substantial number of bird species whose breeding range extends beyond central Mexico (nonendemics). Nonetheless, the empirical pattern that Hawkins and Diniz-Filho (2002) documented for the endemics is interesting and surprising in its own right (their fig. 2) and similar to McCain's (2003) findings for desert rodents. For the endemics considered alone, Hawkins and

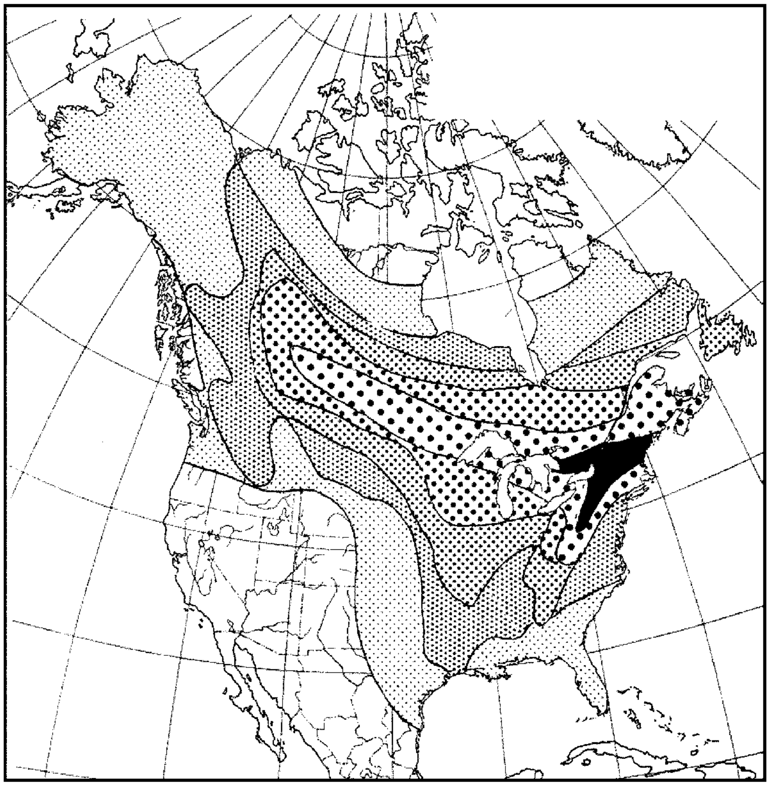

Figure C3: Species richness of North American birds endemic to eastern deciduous forest-taiga; figure from Mengel (1970)

Diniz-Filho's analysis shows that species richness peaks in an east-west band in the latitudinal center of the domain, especially for wide-ranging species, just as MDE models predict. In contrast, for longitude, there is little evidence for a mid-domain peak or plateau for the endemics.

These one-dimensional views are striking and call for explanation. The lack of a longitudinal mid-domain effect may arise from pooling data for birds from distinct faunas inhabiting the eastern forests, the mid-continental grasslands, and the western mountains. The biome-based maps of Mengel (1970) for birds endemic to each of these biomes (reproduced here as figs. C1, C2, C3) strongly suggest that each of these three faunas may show a separate longitudinal MDE (as well as a latitudinal MDE). When richness patterns for the three biomes are combined, they would tend to produce the transcontinental latitudinal MDE revealed by Hawkins's analysis, while the longitudinal MDE for each biome, individually, would be obscured.

Unfortunately, Hawkins and Diniz-Filho (2002, p. 423) dismissed the latitudinal mid-domain peak in the empirical data as an artifact because "bird richness does not actually decrease into Mexico; this just appears to be the case because a large number of bird species … were excluded from the data." Unless some pervasive form of interspecific competition is being implicitly assumed (between endemics as a whole and nonendemics as a whole) to account for the southward decline in the richness of North American endemics, then this explanation makes no more sense than it would make to note that lizards and ants were excluded from the analysis. If climate fully determines latitudinal richness patterns, why should species richness of endemic bird species not peak in the southern reaches of the domain, instead of in its north-south center, as is actually the case?

Biased Data Set Selection: Zapata et al. Zapata et al. (2003, p. 683) suggest that results of empirical studies of MDE are collectively biased since MDE studies "would not have been published in the first place" had there not been "gross similarity between the predictions and patterns actually observed." Leaving aside the fact that a number of studies have appeared for which MDE predictions are poorly supported, some of them published by proponents and others by critics of MDE models (see table 1 and fig. 1), the potential biases introduced into scientific literature by the processes of problem selection, decisions to submit results, and publication decisions of editors are in no way unique to studies of MDE. In short, this does not seem to us to be a useful specific criticism of MDE, or of most other hypotheses, for that matter.

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