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TESTS OF THE MID-DOMAIN HYPOTHESIS: A REVIEW OF THE EVIDENCE

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Abstract. Geographic variation of species richness is strongly correlated with environmental gradients. However, random arrangement of species distributions within a bounded domain can also theoretically produce richness gradients without underlying environmental gradients. This mid-domain effect (MDE) could serve as the null hypothesis against which to test effects of environmental variables, or as a component of a multivariate explanation of species-richness patterns. Recent reviews have concluded that there is a substantial MDE signature in observed geographical patterns of richness, based on correlations between observed patterns of richness and the predictions of mid-domain models. However, the mid-domain hypothesis makes additional powerful predictions about how richness should vary through space, and about the slope of the relationship between predicted and observed richness. Very few studies have tested these more powerful MDE predictions. Here, we reexamine the published mid-domain literature for agreement between observed patterns of richness and MDE predictions. We find that 50 of 53 published studies of MDEs showed significant deviations from the predictions of mid-domain models. When observed richness is correlated with MDE predictions, there are nearly always strongly collinear environmental gradients (e.g., in the Americas, climatic favorability and MDE-predicted richness are both maximal in the middle). Interpolation in sparsely sampled data can also give rise to spurious, apparently strong, mid-domain effects (e.g., the classic study of the Madagascan rain forest). We conclude that observed broad-scale patterns of species richness are not consistent with the mid-domain hypothesis.

Key words: diversity; mid-domain effect literature review; mid-domain hypothesis; species richness.

INTRODUCTION

Species richness varies dramatically over broad spatial scales (e.g., H-Acevedo and Currie 2003). A large literature has sought to relate geographic gradients of species richness to environmental gradients (Rosenzweig 1995, Hawkins et al. 2003). However, Colwell and Hurtt (1994) proposed that spatial patterns of species richness should exist even in the absence of environmental gradients. They noted that, if species' ranges are distributed randomly within a bounded domain, more ranges will overlap in the middle of the domain than at the edges (Colwell and Hurtt 1994). This central maximum of richness was dubbed the "mid-domain effect" (MDE). Colwell and Hurtt proposed that hypothesis tests about environmental influences on species richness should be compared to a spatially defined MDE null model, rather than the conventional statistical null model used in earlier literature.

This proposition could fundamentally change the interpretation of decades of research on determinants of species richness. However, it proved to be controversial on theoretical grounds, and uncertain empirically. The purpose of the present study is to address the question: Are observed patterns of richness consistent with the predictions of the mid-domain hypothesis? To put this question in context, we first briefly review the debate.

A brief recap of the debate

In an early review, Colwell and Lees (2000) summarized the logic of the mid-domain hypothesis. They discussed several methods to derive expected spatial patterns of richness in the absence of environmental gradients, and they noted that mid-domain peaks of richness had been observed in nature (Willig and Lyons 1998, Lees et al. 1999). Colwell and Lees (2000:70) concluded that "the question is not whether geometry affects such patterns, but by how much."

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Mid-domain theorists propose that MDE model predictions should be used in one of two ways. MDE-predicted richness could serve as the null pattern to be removed from observed patterns of richness before testing for environmental effects. That is,

$$R(x, y) - \mathrm{MDE}(x, y) = \mathrm{g}(\mathbf{Z}) + \varepsilon \tag{1}$$

where $R(x, y)$ is species richness at geographic coordinates x and y, $\mathrm{MDE}(x, y)$ is mid-domain predicted richness at x and y, $\mathrm{g}(\mathbf{Z})$ is a function of a vector $\mathbf{Z}$ of environmental variables, and ε is random error (e.g., Connolly et al. 2003). Alternatively, MDE predictions could be used as a candidate explanatory variable, along with environmental variables, in statistical models of spatial variation in richness:

$$R(x, y) = \mathrm{g}(\mathbf{Z}) + \mathrm{MDE}(x, y) + \varepsilon \tag{2}$$

(e.g., Jetz and Rahbek 2001, 2002, Bellwood et al. 2005).

Critics raised several objections (Hawkins and Diniz-Filho 2002, Zapata et al. 2003, 2005, Hawkins et al. 2005). First, MDE models can be formulated in many ways, and different formulations predict different spatial patterns of richness. Which pattern is, in fact, null? Second, MDE predictions are derived by randomizing observed species range sizes. If the area and the cohesiveness of species' ranges reflect responses to environmental variables, then MDE predictions are not null with respect to environmental gradients. Finally, empirical support for MDEs is questionable. Zapata et al. (2003:677) reviewed 11 published MDE studies and concluded that, "most studies do not show a high degree of concordance between observed and predicted species richness patterns, particularly in 2-D [two dimensions]."

Colwell et al. (2004, 2005) re-reviewed the subject and defended the logic of MDE models. Moreover, they concluded that "an overview of the 21 MDE studies published to date reveals a substantial signature of MDE [on richness] in natural patterns and justifies continued work" (Colwell 2004:E1). Similarly, Willig et al. (2003:296), in their review of latitudinal patterns of diversity, list geometric effects among the main candidate explanations of diversity, saying that, "empirical support for the geometric constraints model is increasing."

Support for MDEs takes two forms. First, observed patterns of richness are often significantly correlated with MDE-model-redicted richness (Colwell et al. 2004: Table 1). Second, the mid-domain hypothesis predicts that MDEs will be more pronounced among large-ranged species than among small, because large ranges are more likely to overlap by chance than small ranges. This has repeatedly been observed (Colwell et al. 2004).

Relatively few studies have focused on testing the mid-domain hypothesis (i.e., Is there evidence that is *inconsistent* with the hypothesis?), as opposed to supporting it (i.e., Is evidence *consistent* with the hypothesis?). Mid-domain theory makes powerful testable predictions (P_1–P_5, below) beyond the simple correlation between predicted and observed richness. Since MDE theory proposes that mid-domain peaks of richness must occur in all bounded domains, there are many opportunities for strong tests of the theory.

Strong MDE predictions

P_1.—"MDE outputs are more than correlates of species richness.... 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" (Romdal et al. 2005:238; also Colwell et al. 2004:E13).

P_2.—Observed patterns of richness can be tested statistically for goodness of fit to predicted patterns. This can be done, for example, by Komolgorov-Smirnov tests (e.g., Lees et al. 1999), or by runs tests on the residuals from predicted relationships.

P_3.—The mid-domain hypothesis is completely general: it should apply to all endemic taxa in any bounded domain (e.g., Lees et al. 1999, Cardelús et al. 2006).

P_4.—The expected slope between observed and MDE-predicted richness also constrains the expected correlation. In least-squares regression of $A = f(B)$, where A and B are any two variables, the slope $b_{A.B}$ and the correlation coefficient r_{AB} are related to one another by definition:

$$r_{AB} = b_{B.A} \frac{s_A}{s_B}$$

where s_A and s_B are the standard deviations of A and B. Mid-domain theory requires that the slope of observed richness as a function of MDE-predicted richness must be 1.0 (see P_1). Mid-domain theory therefore also predicts that the proportion of variance explained by an MDE model (r^2_{AB}) must be

$$r^2_{AB} = \frac{s^2_A}{s^2_B} = \frac{\text{Variance(predicted richness)}}{\text{Variance(observed richness)}}. \tag{3}$$

This prediction has a surprising corollary. Because MDE-predicted richness is derived by randomizing observed species' ranges, the variances of predicted and observed richness in a given domain tend to be similar (Zapata et al. 2003:683, Colwell et al. 2004:E8). Consequently r^2_{AB} should be near 1 in most cases. In other words, MDEs should explain almost all the variance in observed richness in nature.

P_5.—Predicted mid-domain peaks are two-dimensional, and approximately radially symmetrical, although the exact shape depends upon the shape of the domain (e.g., Colwell and Lees 2000: Fig. 1, Jetz and Rahbek 2001: Figs. 1 and 2b, Kerr et al. 2006: Fig. 1).

METHODS

We searched the Web of Science on 26 April 2007 for the phrase "mid-domain." Web of Science returned 70 studies. Among these, 53 studies compared MDE-predicted and observed richness, or they presented data

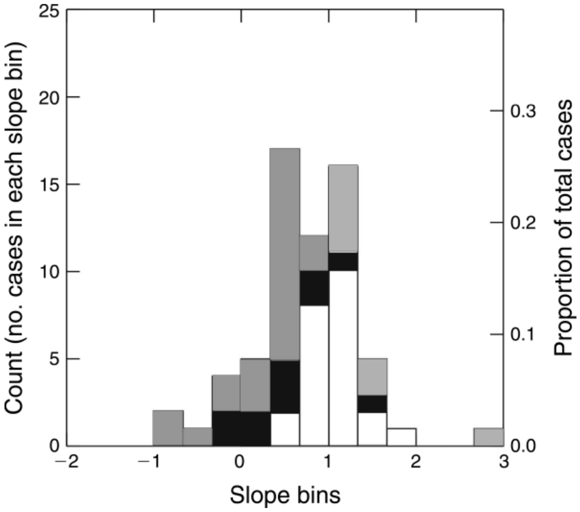

FIG. 1. In 65 studies of a taxon in a given domain (e.g., African birds, Himalayan plants), the frequency distribution of observed slopes of the relationship between observed and predicted richness. Count is the number of cases with a slope in each of the bins on the abscissa. Theory predicts that the slope should equal 1.0. Cases with slopes that do not differ significantly from 1.0 are unshaded. Slopes that do not differ significantly from 0.0 (i.e., no significant relationship) are black. Slopes that do differ significantly from 1.0 are gray. Sixty-four percent of these slopes are inconsistent with the mid-domain predictions.

that allowed us to do so (Table 1). The remaining papers included review articles, theoretical or modeling studies, and studies in unrelated fields.

When an article included figures showing observed- and MDE-predicted richness, we digitized the data using TECHDIG version 2 software (R. Jones, *unpublished software*). For the digitized data set we calculated the slope of observed vs. predicted richness. We considered the slope to be consistent with MDE prediction if it was significantly different from 0.0, and not significantly different from the predicted value of 1.0 ($\alpha = 0.05$). For one-dimensional gradients (e.g., latitude, elevation, depth), we used a runs test to detect pattern in the residuals (i.e., a test of goodness of fit). We also calculated the predicted correlation (P_4) and the observed correlation. Finally, in each study, we noted the authors' own observations about agreement between predicted and observed patterns.

Many studies compared observed and MDE-predicted richness for several taxa, or using several different null models. When tests involved different taxa, we recorded the taxa separately, unless the taxa were nested (e.g., a family and its subfamilies). In that case, we recorded only the results from the highest taxonomic level. When studies used multiple MDE models (based on different assumptions) to calculate predicted richness, we used predicted richness obtained by randomizing observed species' ranges.

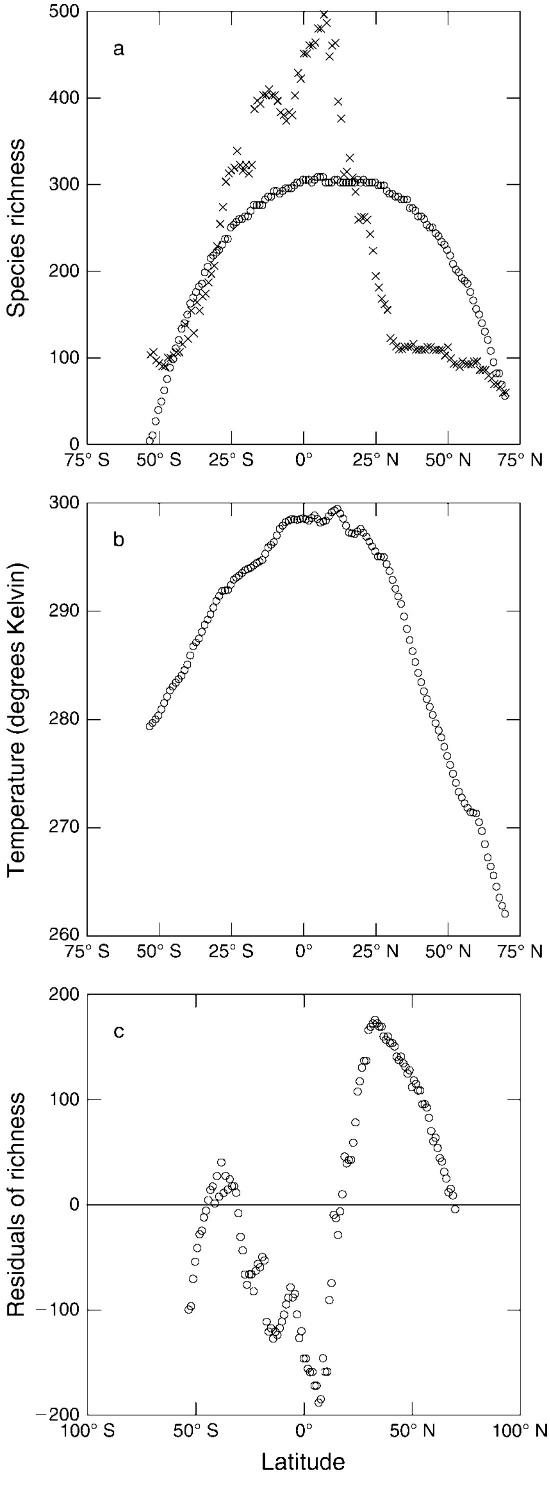

FIG. 2. (a) Using data digitized from Romdal et al. (2005: Fig. 1a), the richness of breeding birds in 1° latitudinal bands in the New World (×), and the predicted richness from a one-dimensional mid-domain model (○). (b) The latitudinal variation of mean annual temperature, averaged across latitudinal bands (data from Francis and Currie [2003]). (c) The residuals from mid-domain predicted richness.

TABLE 1. A summary of studies presenting data that permit tests of predictions of the mid-domain hypothesis; the taxa and the domain examined in the original study are listed. Boldface indicates observations inconsistent with the predictions of the mid-domain effect (MDE); italics indicate conditions that weaken tests of the MDE.

				Environ. variables†			
Reference	Taxa	Gradient	Domain	Climate and/or productivity	Area	MDE model‡	Inter-polation§
Horizontal (geographic) patterns of richness							
Willig and Lyons (1998)	bats marsupials	lat.	New World	*no*	*no*	yes	RM
Lees et al. (1999)	mycalesines and other taxa	lat. 2-D	Madagascan rainforest biome	*no* yes	yes yes	yes yes	*yes* *yes*
Bokma et al. (2001)	mammals	lat.	New World	*no*	*no*	yes	??
Jetz and Rahbek (2001)	birds	lat. long. 2-D lat. 2-D long.	Sub-Saharan Africa	*no*	no no n/a	yes	no (?)
Koleff and Gaston (2001)	parrots woodpeckers	lat.	New World	*no*	yes	yes	RM
Diniz-Filho et al. (2002)	Falconiformes Strigiformes	2-D	South America	*no*	n/a	yes	RM
Ellison (2002)	mangroves	lat.	global	*Precip., not temp.*	yes	yes	no
Hawkins and Diniz-Filho (2002)	birds	2-D	North America	*no*	n/a	yes	RM
Jetz and Rahbek (2002)	birds	2-D	sub-Saharan Africa	yes	n/a	yes	no (?)
Laurie and Silander (2002)	Proteaceae	lat.	Cape floristic province	*no*	n/a	yes	no
Connolly et al. (2003)	corals fish corals fish	lat. lat. long. long.	Indo-Pacific	*no*	*no*	yes	*yes*
McCain (2003)	rodents	lat.	Western American deserts	*no*	yes; see Note	yes	RM
Rangel and Diniz-Filho (2003)	Falconiformes	2-D	global	yes	n/a	yes	RM
Aliabadian et al. (2005)	contact zones of parapatric passerine birds	2-D	Palaearctic	*no*	n/a	yes	RM
Arita et al. (2005)	bats	lat.	North America	*no*	*no*	yes	RM
Bellwood et al. (2005)	corals, fish	2-D	Indo-Pacific	yes	yes	yes	No
Ferrer-Castán and Vetaas (2005)	pteridophytes	2-D	Iberian peninsula	yes	n/a	*no*	RM
Hernández et al. (2005)	benthic polychaetes	lat.	Chilean coast	*no*	n/a	yes	*yes*
Mora and Robertson (2005)	shore fishes	lat.	Tropical Eastern Pacific	yes	n/a	yes	*yes*
Romdal et al. (2005)	birds	lat.	New World	*no*	yes	yes	??
Smith et al. (2005)	*Acaris* hylids hylids *Hyla*	2-D	N. America Asia Europe N. America	*no*	n/a	yes	*RM*
Kerr et al. (2006)	mammals birds birds	lat. lat. 2-D	Madagascar	yes	n/a	yes	*RM*
Moreno et al. (2006)	polychaetes	lat.	Chile (18°–56° S)	*no*	*no*	yes	*yes*
Storch et al. (2006)	birds	2-D	global	yes	n/a	yes	*yes*
Rahbek et al. (2007)	birds	2-D	South America	yes	n/a	yes	yes

TABLE 1. Extended.

r^2||		Obs. slope, b¶	Runs test P#	Notes
Exp.	Obs.			
0.45	0.68	**1.24**[a]	**$<10^{-4}$**	*Mid-latitude peak in richness is collinear with temperature.*
0.82	*0.35*	**0.08**[a]	**$<10^{-4}$**	
0.88	0.89	1.00	**0.004**	**MDE-predicted and observed richness fit $P < 10^{-3}$ (1-D models, all species; their Table 5).** Acceptable fit for some other groups. ***2-D predicted values are nearly all greater than observed (their Fig. 11; binomial test $P < 10^{-5}$).*** *Most observations in mid-domain peak are interpolated (p. 539).*
0.88	0.78	0.93	**$<10^{-3}$**	
0.62	*0.14*	**0.48**[a]	**$<10^{-4}$**	"**Our model could not explain latitudinal variation in species richness of New World mammals**" (p. 43).
0.87	0.66	0.87	**$<10^{-4}$**	The authors conclude that, "Latitudinal, longitudinal, and two-dimensional patterns of species richness are well-predicted from the modeled null effects alone" (p. 5661). **However, their tests of fit (their Table 1) agree only with latitudinal data. For 2-D models, there is negligible probability ($<10^{-4}$) of agreement with observed patterns.** *Collinearity problems as well.* (See Appendix C.)
0.83	0.61	0.85	**$<10^{-4}$**	
0.43	0.63	1.21	**$<10^{-4}$**	
0.78	0.56	0.85	**$<10^{-4}$**	
1.71	0.97	**0.75**[a]	**0.02**	**5° bands of latitude. "...the fit of these [MDE] models is uniformly poor" (**p. 341).
2.45	0.94	**0.62**[a]	**0.001**	
n/a	**0.05**[c] **0.02**	n/a	n/a	"**The correlation between observed richness and expected richness** ... **was very low**" (p. 50). Richness variation related to habitat heterogeneity.
0.78	0.78	1.00	>0.1	Latitudinal variation in SR agrees with MDE predictions. **However, "the latitudinal pattern ... is due almost entirely to mangrove area at a given latitude**..." (p. 186). *Low statistical power: n = 14.*
n/a	0.21[c]	**n/a,**[c] but **$P < 10^{-2}$**	n/a	"**The observed pattern of bird richness clearly varied from that predicted by both geometric models.**" *Collinear gradients.* (See Appendix C.)
n/a	*0.18*	n/a	n/a	*MDE significant, "but its strength compared to productivity and habitat heterogeneity is relatively low"* (p. 1549). *Collinear precipition gradient.* (See Appendix C.)
1.49	0.33	**0.47**[a]	**$<10^{-4}$**	"**Geometric constraint does not explain the spatial pattern in this case**" (p. 351).
0.69	0.87	**1.12**[a]	**$<10^{-4}$**	"**Longitudinally, coral and fish species-richness** ... **differ markedly from mid-domain predictions.** Latitudinally, agreement ... appears much closer" (p. 2181). *However, currents and temperature are collinear with the mid-domain in the Pacific and Indian oceans.* (See *Discussion: Collinearity on geographic gradients.*)
0.56		**1.30**[a]	**$<10^{-4}$**	
0.59		0.83	**$<10^{-4}$**	
0.45		1.08	**$<10^{-4}$**	
0.61	0.86	**1.19**[a]	**$<10^{-4}$**	"Observed species richness is highly correlated with predictions of the binomial model (r^2 = 93%) **but does not generally occur within 95% confidence intervals**..." (p. 967).
n/a	**0.00**[c]	n/a	n/a	"**Only 0.2% of the variation in species richness can be explained by GCM** [geometric constraints model] **predictions**" (p. 206).
n/a	0.04[c]	n/a	n/a	"**A mid-domain effect null model** ... **had low explanatory power of 3.8**%" (p. 21). *No test of goodness of fit.*
0.09	**0.01**[b]	**−0.31**[b]	**$<10^{-3}$**	**Observed variation of richness and range size "deviated sharply from null models"** (p. 961).
n/a	n/a	n/a	n/a	Best model includes MDE and area. *MDE prediction is strongly collinear with area and temperature (and currents?).* (See *Discussion: Collinearity on geographic gradients.*)
n/a	n/a	n/a	n/a	"**Richness is significantly higher along the coast than in the centre of the peninsula**" (p. 155).
1.03	0.40	0.62	>0.1	"... *richness increased toward southern latitudes.* ... [There is] a weak level of mid-domain effect on species richness" (p. 363). *Low statistical power: n = 13.*
0.89	0.91	1.01	**$<10^{-4}$**	Observed peak in richness close to MDE predictions. However, MDE is strongly collinear with mean temperature: $r = 0.96$. (See Appendix C.)
0.25	0.43	**1.33**[a]	**$<10^{-4}$**	**Temperature is a better predictor of richness than MDE.** (See *Discussion: Collinearity on geographic gradients*; also see Appendix A.) After controlling for area, MDE passes the slope test, but **fails the runs test.**
0.16	0.49	**2.68**[a]	low n	Mid-latitude peaks of richness. *Very low statistical power: n < 10.*
0.06	0.02	**0.59**[b]	low n	
0.22	0.74	1.83	low n	
0.14	0.20	**1.59**[b]	low n	
0.76	0.76	1.00	**$<10^{-3}$**	**Richness shows a mid-domain minimum.**
1.88	0.16	**0.29**[a]	**$<10^{-3}$**	
0.27	<**0**	**−1.0**[a]	**$<10^{-4}$**	
0.38	0.73	1.40	low n	Richness peaks in the mid-domain; **however, 5 of 13 observations differ significantly ($P <$ 0.05) from the MDE predictions.** *Collinearity with temperature southward; artificial (political) northern domain boundary boundary. Low statistical power: n = 13.*
n/a	n/a	n/a	n/a	"**[An MDE model] constrained only by the distribution of continental masses did not predict observed patterns of species richness**" (p. 1313). Within-biome MDE and actual evapotranspiration statistically explain indistinguishable amounts of variance. No tests of goodness of fit.
n/a	**0.16**[b,c]	1.19[c]	n/a	**Richness is not significantly correlated with MDE prediction.**

TABLE 1. Continued.

Reference	Taxa	Gradient	Domain	Environ. variables†			
				Climate and/or productivity	Area	MDE model‡	Interpolation§
Vertical patterns of richness							
Rahbek (1997)	birds	elevation	South America, divided into 7 elevation bands	*no*	yes	no	no
Fleishman et al. (1998)	butterflies	elevation	Nevada	yes	yes	yes	no
Pineda and Caswell (1998)	gastropods, polychaetes	depth	NW Atlantic	*no*	*no*	yes	*yes* (?)
Lees et al. (1999)	mycalesines	elevation	Madagascar	*no*	yes	yes	*yes*
Kessler (2001)	pteridophytes and angiosperm families	elevation	Bolivia	yes: PET	n/a	yes	no
Grytnes and Vetaas (2002)	vascular plants	elevation	Nepalese Himalayas	*no*	*no*	yes	*yes*
Sanders (2002)	ants	elevation	Colorado, Nevada, Utah	*no*	yes	partially	*yes* (?)
Smith and Brown (2002)	pelagic fish	depth	North Pacific	*no*	*no*	*no*	*yes*
Grytnes (2003*a*)	vascular plants	elevation	seven transects in Norway	*no*	n/a	*no*	no
Bachman et al. (2004)	plants	elevation	New Guinea	*no*	yes	yes	*yes* (?)
McCain (2004)	non-volant small mammals	elevation	one transect in Costa Rica	*no*	n/a	yes	no
Carpenter (2005)	plants	elevation	Western Nepalese Himalayas	yes	yes	yes	no
Herzog et al. (2005)	birds	elevation	Bolivean Andes	*no*	yes	yes	no
Krömer et al. (2005)	Vascular epiphytes	elevation	Bolivean Andes	yes	n/a	yes	no
McCain (2005)	non-volant small mammals	elevation	meta-analysis of 56 data sets	n/a	n/a	yes	n/a
McClain and Etter (2005)	bivalves gastropods polychaetes	depth	western North Atlantic	*no*	*no*	yes	no
Mena and Vázquez-Dominguez (2005)	rodents	elevation	13 gradients worldwide	*no*	*no*	yes	no
Oommen and Shanker (2005)	tropical plants temperate plants	elevation	geopolitical units in the Himalayas	yes	yes	yes	*yes*
Almeida-Neto et al. (2006)	harvestmen (Arachnida)	elevation	SE Brazil	yes	*no*	yes	no
Cardelús et al. (2006)	epiphytes aroids bromeliads ferns orchids	elevation	Barva transect, Costa Rica	yes and no	n/a	yes	no
Dunn et al. (2006)	shoreline plants	along the river axis	Kalix River Torne River	*no*	yes	yes	no

TABLE 1. Continued, Extended.

r^2||		Obs.	Runs	
Exp.	Obs.	slope, b¶	test P#	Notes
n/a	n/a	n/a	n/a	**Richness decreases monotonically with elevation.** *Controlling for area, richness peaks in second-lowest elevational band (of 7).*
n/a	n/a	n/a	n/a	**Weak correlation. "The observed distribution of species richness was significantly different from the distribution expected under our null model assumptions"** (p. 2487).
n/a	n/a	n/a	n/a	**No mid-domain peak in richness. "Overall we find that random rearrangements cannot explain most characteristics of the parabolic diversity patterns of gastropods and polychaetes [in samples rarified to contain equal numbers of individuals]"** (p. 83).
1.49	0.57	**0.62**[a]	>0.1	*"All the curves [of richness as a function of elevation] in Fig. 7 differ significantly in central tendency from the null model"* (p. 550).
n/a	n/a	n/a	n/a	**Significant correlation between observed and MDE-predicted richness for only 3 of 8 plant groups. Richness of 5 of 8 groups decreases monotonically with elevation.** Diversity varies with productivity.
n/a	n/a	n/a	n/a	*Generated MDE model, but no statistical tests of fit.* Concluded that richness is influenced by a combination of MDE, climate and interpolation. *Collinear with climate and area.* (See Appendix C.)
0.31	0.33	1.04	$\mathbf{<10^{-4}}$	Mid-elevation peaks in richness, *at lower elevation and more peaked than predicted.* Area explained most of the pattern; significant residual MDE correlation
0.45	0.90	**1.41**[a]	**0.02**	
0.25	0.32	1.13	$\mathbf{<10^{-4}}$	
n/a	n/a	n/a	n/a	**Maximum richness near surface. "Results reject [the hypotheses] that would attribute the pattern of species richness to the mid-domain effect"** (p. 213).
n/a	n/a	n/a	n/a	**"In five [southern] transects species richness peaked at mid-altitudes, whereas in the two northern transects species richness decreased with altitude"** (p. 291). *Collinear climate and area.* (See Appendices A and C.)
0.56	0.27	**−0.69**[a]	$\mathbf{<10^{-4}}$	Richness decreases with elevation. "… [W]hen assessed in equal-area bands, species richness shows a pronounced mid-elevation peak" (p. 299). *However the peak occurs at an elevation of 21–48 m on a gradient of 0–5030 m.* (See Appendices A and C.)
1.30	0.46	**0.52**[a]	**0.02**	*"The moderate fit to the null model predictions were demonstrated by the low* r^2 *values (alpha* $r^2 = 0.482$*; gamma* $r^2 = 0.454$*), although climatic conditions including an intermediate rainfall and temperature regime, and distance from the persistent cloud cap are also correlated with the pattern of species richness"* (p. 19).
n/a	n/a	n/a	n/a	**"Neither mid-domain effects nor biologically valid boundary effects like dispersal limitation explain the plant species density trends observed. Trends do fit a model in which species density is controlled by the same 'active' climatic variables that predict species richness on continental scales"** (p. 999). (See also Appendix C.)
1.51	0.43	**−0.53**[a]	**0.004**	Local species richness peaked at ~1000 m elevation, but "**the correlation to MDE in the multiple regression was likely spurious**" (p. 222) due to other collinear factors. *Low statistical power:* $n = 12$*.* (See also Appendix C.)
n/a	n/a	n/a	n/a	**"The hump-shaped richness pattern differed from a null-model of random species distribution** …" (p. 1799). *Precipitation also shows mid-domain peak, and "We hypothesize that the decline of richness at high elevations is a result of low temperatures"* (p. 1799).
n/a	n/a	n/a	n/a	**"Very few data sets fit entirely within the predictions of the null model, and the average predictive power of the null model was low"** (p. 555).
0.16	0.41	1.58	>0.1	"**Bathymetric patterns of species diversity for gastropods, bivalves and polychaetes differ substantially from null expectations**…" (p. 555).
0.23	**0.09**[b]	0.63	>0.1	
4.71	**0.00**[b]	**−0.01**[b]	**0.006**	
n/a	n/a	n/a	n/a	"**Observed and predicted species turnover** [beta diversity] **were statistically different**" (p. 539).
0.46	0.53	1.07	**0.002**	"**There was a significant correlation with the predictions of the mid-domain model in Chamoli District, but not in Uttaranchal State or Western Himalaya**…" and "… temperate species richness followed mid-domain predictions, *and showed a non-linear relationship with temperature*, **whereas tropical species richness tracked temperature and area**" (p. 3043).
0.94	0.89	0.97	**0.009**	
0.66	0.00	**−0.08**[a]	**0.02**	**Richness decreases with elevation.**
1.08	0.81	0.87	low n	Relationship peaked for ferns, orchids, and bromeliads, **but not for aroids.** For all epiphytes, relationship is peaked, **but 4 of 6 sites fall outside of predicted 95% confidence envelope.** *Climate predicts richness as well, or better than, MDE. Low statistical power:* $n = 6$*.*
0.60	0.00	**0.06**[b]	low n	
0.83	0.48	**0.76**[b]	low n	
1.55	0.84	0.74	low n	
0.91	0.99	**0.70**[a]	low n	
1.34	0.29	**0.46**[a]	*0.08*	Richness of non-ruderal species shows a mid-river peak, **but ruderal and total richness do not. The slopes and intercepts of the observed-predicted relationships differ significantly from expected values.** (See *Discussion: Collinearity in a river domain.*)
1.13	0.05	**0.21**[a]	>0.1	

TABLE 1. Continued.

				Environ. variables†			
Reference	Taxa	Gradient	Domain	Climate and/or productivity	Area	MDE model‡	Inter-polation§
Fu et al. (2006)	all frogs frogs, regionally endemic	elevation	Hengduan Mountains	yes	yes	yes	*yes*
Jankowski and Weyhenmeyer (2006)	phytoplankton	lakes along elevation gradients	50 Swedish lakes	*no*	yes	yes	no
Kendall and Haedrich (2006)	fishes	depth	Atlantic Denmark Strait Faroe–Iceland ridge Gulf of Mexico s. New England	*no*	*no*	yes	*yes* (?)
Kluge et al. (2006)	pteridophytes	elevation	Barva transect, Costa Rica	yes	n/a	yes	no
Watkins et al. (2006)	canopy epiphytes trunk epiphytes ground spp.	elevation	Barva transect, Costa Rica	yes	n/a	yes	*yes*
Brehm et al. (2007)	geometrid moths	elevation	Barva transect	yes	n/a	yes	*yes*
McCain (2007)	bats	elevation	meta-analysis of 27 gradients worldwide	*no*	*no*	*no*	??

Notes: Horizontal lines are included as visual aids only. Details for sources of data and analyses are presented in Appendix A. Abbreviations: lat. = latitude, long. = longitude, 2-D = two dimensional, n/a = not applicable.

† The columns headed "Environ. variables" note whether the study explicitly tested for effects of climate or productivity or area (because these are the environmental variables most commonly observed to be correlated with spatial patterns of richness; Hawkins et al. 2003). PET = potential evapotranspiration.

‡ MDE model notes whether quantitative predictions of a mid-domain model were derived (vs. simply looking for peaked functions of domain coordinates).

§ Interpolation notes whether range continuity was assumed across cells of missing information. "RM" in this column indicates that diversity is based upon range maps, which involve unknown amounts of interpolation.

|| Exp. r^2 is the expected coefficient of determination between observed richness and richness predicted from the mid-domain model. Obs. r^2 is the observed coefficient of determination.

¶ The expected slope of the relationship between predicted and observed is 1.0; the observed slope is given under b.

The runs test determined whether successive residuals around a model tend to have the same sign. Runs tests were not carried out when $n < 15$, due to low statistical power (cells designated "low n").

[a] Test of the hypothesis that $b = 1.0$: $P < 0.05$.

[b] Test of the hypothesis that $b = 0.0$: $P > 0.05$.

[c] The data are not shown in the original paper, but the statistic is reported.

In some studies, it was impossible to extract the original data. Sometimes the data were not shown. In a few other cases, data were so numerous that individual points could not be distinguished in the printed figures (e.g., Storch et al. 2006: Fig. 2). Also, some studies did not use an explicit MDE model to derive predicted richness; instead, they tested for a peak of richness within a specified domain. In all these cases, we simply noted the authors' conclusions about agreement between observed richness and MDE predictions. Details on the sources of data are given in Appendix A.

We present the results of individual statistical tests in Table 1. To summarize, we report the number of studies (i.e., papers; $n \leq 53$) or the number of cases (a particular taxon in a given domain; $n \leq 95$) that yielded a particular result. Sample sizes for different tests differ because not all studies reported the data for all tests.

RESULTS

Among the 53 studies that compared observed- and MDE-predicted patterns of richness, 49% stated explicitly: (a) that MDE predictions did not statistically explain significant amounts of variance in richness, (b) that observed patterns of richness differed significantly from MDE model predictions (P_1), and/or (c) that statistical fit was consistent with model predictions for some groups of organisms but inconsistent for others (P_3) (Table 1, last column). These are the authors' own assessments, often based upon tests of fit between predicted and observed values, or simply lack of the predicted mid-domain peak in richness.

A further 45% of the studies either carried out these same tests and show evidence inconsistent with the mid-domain hypothesis without arriving at that conclusion,

TABLE 1. Continued, Extended.

r^2‖		Obs. slope, b¶	Runs test P#	Notes
Exp.	Obs.			
0.48	0.20	1.19	**$<10^{-4}$**	**Out of 23 observations, 20 fell outside 95% MDE-predicted confidence limits for all species, as did 9 of 23 for regionally endemic species.**
0.79	0.30	**1.62^{a}**	**0.003**	
2.01	0.62	**0.55^{a}**	low n	**Richness per lake decreases monotonically with elevation.** Richness per latitudinal band, divided by the number of lakes per band is a peaked function of elevation, **but much lower than the MDE model prediction.** *The number of lakes per band decreases strongly with elevation. Low statistical power: $n = 7$.*
0.07	0.02	**0.59^{b}**	**0.001**	**The observed patterns show a decline in richness with depth, and do not match the richness patterns produced by the null model.** *Low statistical power (n = 10–14).*
0.69	0.03	**-0.22^{a}**	*0.08*	
1.21	0.27	**0.47^{ab}**	*0.08*	
0.70	0.00	**0.33^{ab}**	**0.01**	
0.21	0.17	**0.89^{b}**	**0.01**	
5.14	0.66	$0.35^{\mathbf{a}}$	**$<10^{-4}$**	*"While geometric models explained much of the pattern in species richness, we cannot rule out the role of climatic factors (or vice versa) because the predicted peak in richness from geometric models, the empirical peak in richness, and the overlap in favorable environmental conditions all coincide at middle elevations"* (p. 358). **Significant lack of fit for both large- and small-ranged species.** $n = 27$.
2.80	0.90	**0.57^{a}**	low n	**Observed richness falls outside of 95% predicted confidence interval for 50% of sites for all epiphytes and for canopy epiphytes, and at 33% of sites for trunk epiphytes and ground species**. *Climate predicts richness as well, or better than, MDE. Low statistical power: $n = 6$.*
2.73	0.83	**0.55^{a}**	low n	
3.18	0.67	**0.46^{a}**	low n	
3.23	0.95	**0.54^{a}**	low n	**Out of 6 observations, 3 fall outside 95% MDEpredicted confidence limits.** *Climate predicts richness as well, or better than, MDE. Low statistical power: $n = 6$.*
n/a	n/a	n/a	n/a	"**Null model analyses reveal bat elevational richness is not responding simply to spatial constraints . . .. Meta-analyses pinpoint the combination of temperature and water availability as the key driving factors**" (p. 9).

or analysis of their data leads us to do so (Table 1). Among the 65 cases in which we could calculate a slope (or one was reported by the authors: P_1), 65% either differed significantly from the expected value of 1.0, or they did not differ significantly from 0.0 (Fig. 1). In general, most slopes (66%) were lower than predicted by the mid-domain hypothesis. In other words, observed gradients of richness are generally less strong than predicted gradients.

Even more commonly, the relationship between observed and MDE-predicted richness shows striking pattern in the residuals (P_2). For example, in the data of Romdal et al. (2004), the residuals over the southern part of the domain are nearly all positive, while the residuals over the northern part of the domain are negative (Fig. 2). We could test goodness of fit using runs tests in 48 cases in Table 1. Observed richness differed significantly ($P < 0.05$) from predicted richness in 40 cases (i.e., 83%). In six of the remaining cases, statistical power may simply have been too low ($n < 15$) to detect lack of fit. For $n < 10$, we did not carry out runs tests.

In 16 of the 97 individual comparisons reported in Table 1, we found no evidence that the observed patterns differed significantly from predicted. However, no study—0%—that examined multiple taxa in a single domain found consistent agreement with MDE predictions for all taxa, in contrast with P_3.

The r^2 values predicted by mid-domain theory (P_4) are also problematic on two levels. First, knowing the variance of observed richness, the variance of MDE-predicted richness, one can calculate the r^2 predicted by mid-domain theory (Eq. 3). In nearly one third of published cases, the mid-domain effect should explain >100% of the observed variation in richness. This is clearly impossible. The median expected r^2 from the studies listed in Table 1 is 0.79. This point is not widely recognized: mid-domain theory predicts that MDEs should account for nearly all the observed broad-scale variation in species richness. There is little remaining room for environmental effects. Observed correlations are much weaker (median $r^2 = 0.46$). Examining all available cases together, observed r^2 values are not significantly related to what MDE theory predicts: $r = 0.23$ ($n = 65$, $P = 0.07$) (Fig. 3).

Two-dimensional patterns: P_5

Zapata et al. (2003) and Colwell et al. (2004:E12–E13) agree that two-dimensional MDE model predictions agree poorly with observed patterns of richness (low explained r^2). Studies that have examined both latitudinal and longitudinal gradients have invariably found much poorer agreement in the longitudinal dimension. In contrast, the MDE predicts similar gradients in all directions (e.g., Jetz and Rahbek 2001, Ellison 2002, Hawkins and Diniz-Filho 2002: Fig. 2, Connolly et al. 2003, Kerr et al. 2006).

Among the 53 studies we reviewed, only two showed both longitudinal and latitudinal maxima of richness. Connolly et al. (2003) studied Indo-Pacific corals and

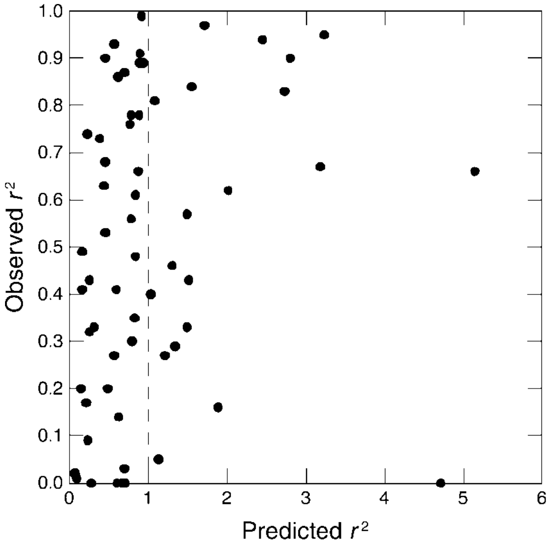

FIG. 3. In 60 cases of a taxon in a given domain, the observed coefficient of determination (r^2) plotted as a function of the predicted coefficient of determination (derived from the observed variances of observed and mid-domain predicted richness). Predicted $r^2 > 1$ (to the right of the dashed line) is clearly impossible; these cases are inconsistent with the mid-domain hypothesis. Overall, the amount of variance that is attributable to mid-domain effects (MDE) is not significantly correlated with the amount that is predicted to occur ($r = 0.23$, $P = 0.07$).

fishes and found strong mid-domain peaks of richness in the western Pacific. Jetz and Rahbek's (2002) examined bird richness in sub-Saharan Africa and found a statistically significant, but weak, correlation between predicted and observed richness.

Continental-scale variations in species richness have been cited as evidence in support of mid-domain effects. In the New World, there is a striking equatorial peak in richness, which Romdal et al. (2005:242) argue "support[s] the hypothesis that distribution of species ranges may be influenced by geometric constraints" (see also Willig and Lyons 1998).

However, no other continent shows strong latitudinal peaks of richness, and none shows a longitudinal mid-domain peak. Continental and global-scale maps of richness Appendix B) show that the richness of most Asian taxa is maximal in the southeast, with a minimum in the central steppes and deserts. Australian richness is generally maximal on the northeast coast, with minima in the central Outback. European richness is maximal in the south. North American richness is low in the central plains, and higher near the coasts. South American richness is highest in peripheral mountainous areas. For taxon-specific details, see Appendix B.

To summarize the evidence, observed patterns of richness often correlate to some degree with MDE model predictions, but they are rarely consistent with any of the stronger predictions of the theory. The slope of the observed–predicted relationship is usually different from the expected value of 1.0. The residuals are almost always spatially structured. Two-dimensional MDEs are not generally observed. A latitudinal MDE is observed in the New World, but not the predicted longitudinal peak, and no other continent shows a mid-domain peak of richness with respect to either latitude or longitude. No study that examined multiple taxa in a given domain observed an MDE for all taxa.

DISCUSSION

A review of the mid-domain literature shows that broad-scale patterns of richness are sometimes consistent with the weakest prediction of the mid-domain hypothesis: greater richness in the middle of domain than at the periphery. Tests of the stronger mid-domain predictions nearly always fail. This raises the following questions.

Why does observed richness sometimes correlate strongly with MDE (mid-domain effect) predictions?

Collinearity on geographic gradients.—Environmental explanations for broad-scale richness gradients most often postulate effects of area, habitat diversity, and/or climate (temperature, precipitation, and/or primary productivity) (Kerr et al. 2001, Hawkins et al. 2003, Willig et al. 2003). Reviewing the published examples of strong MDEs, nearly all of them occurred when MDE predictions were strongly collinear with environmental gradients.

Consider again, for example, Romdal et al.'s (2005) study of bird richness across the Americas. An MDE model predicts maximal richness near the equator. However, temperature also peaks near the equator (Fig. 2b, estimated using data from Legates and Willmott [1992]). Consequently, temperature and the MDE predictions are very strongly collinear along purely north–south gradients ($r = 0.84$). As might be expected, richness peaks near the equator (Fig. 2a). The MDE model statistically accounts for 47% of the variance in area-adjusted species richness, while a quadratic function of temperature accounts for 81.5% ($n = 124$ latitudinal bands, $P < 10^{-5}$). More importantly, a multiple regression of richness as a function of both temperature and MDE accounts for no more variance ($R^2 = 0.818$) than temperature alone (Fig. 4b). Consequently, there is no statistical reason to attribute variation in bird richness to a mid-domain effect, rather than to temperature.

Similarly, Connolly et al. (2003) and Bellwood et al. (2005) proposed MDE models that predicted both latitudinal and longitudinal gradients in the diversity of corals and reef fishes in the Indo-Pacific. However, there is again a collinearity problem. Diversity of corals and reef fishes is greatest where reef area is greatest (Bellwood et al. 2005). The collinearity of area and MDE is nearly perfect (Fig. 4d). The predictions of the MDE model are also collinear with temperature and currents, two other factors to which coral richness is strongly correlated (Fraser and Currie 1996, Connolly et

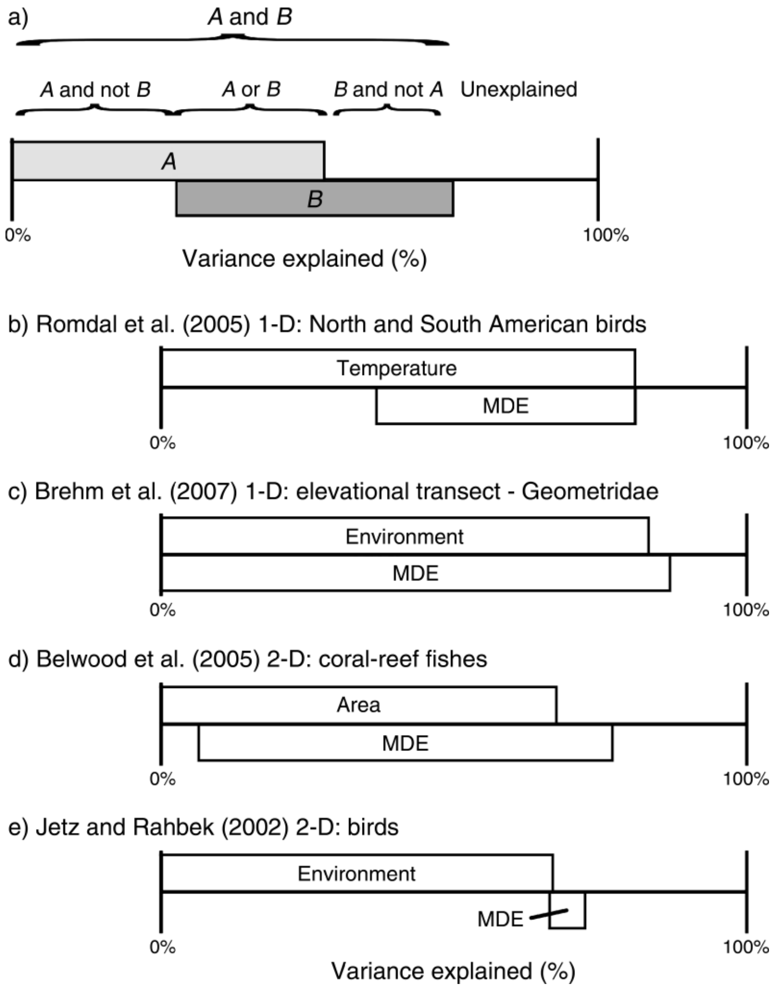

FIG. 4. (a) Partitioning explained variance. In multiple regressions with collinear independent variables *A* and *B*, one can partition explained variance into components. Component "*A* and *B*" is the R^2 of richness as a function of both independent variables. Components "*A*" and "*B*" are the R^2 of richness as functions of *A* or *B*, separately. Other components are calculated by difference. (b–d) In many mid-domain studies (Table 1), mid-domain effect (MDE) predictions are strongly collinear with environmental variables. Consequently, mid-domain effects cannot be distinguished from effects of environmental variables; in (c) "Environment" included temperature, humidity, rainfall, and tree species richness; in (d) "Environment" was net primary productivity and habitat heterogeneity. (e) In the cases where MDE and environment are not strongly collinear, MDE explains relatively little variance. We found *no* published case in which MDE was shown to explain a large amount of variance independently of environmental variables.

al. 2003). Appendix C discusses similar collinearity problems in the studies of Willig and Lyons (1998), Jetz and Rahbek (2001), Ellison (2002), Hawkins and Diniz-Filho (2002), and Mora and Robertson (2005).

Collinearity on elevational gradients.—Studies of MDEs on elevation gradients are similarly confounded by collinear environmental gradients. MDE models predict a mid-elevation peak in richness. Environmental hypotheses often predict a richness peak where actual evapotranspiration (AET; Currie and Paquin 1987), a water × temperature interaction (Francis and Currie 2003), and/or area are maximal. Temperature decreases with elevation (McCain 2004). Precipitation often increases with elevation, or shows a mid-elevation peak (Hay 1998, McCain 2004). Consequently, in many cases, AET will peak mid-slope. In mountainous regions, area within elevational bands can also be a peaked function of elevation (e.g., Grytnes and Vetaas 2002). Consequently the elevational mid-domain is often where climate is often most favorable, and area the largest.

For example, a series of recent studies examined richness on the slopes of the Barva volcano in Costa Rica (Cardelús et al. 2006, Watkins et al. 2006, Brehm et al. 2007). In all of these cases, MDE-predicted richness is very strongly collinear with temperature, precipitation, and a temperature × precipitation interaction (Fig. 4c). This strong collinearity, and low statistical power ($n = 6$ sites) make it impossible to distinguish between MDE vs. environmental effects in these studies (see Appendix A for statistical details).

McCain's (2007) meta-analysis of 27 elevational gradients of bat richness does partially disentangle MDE predictions and environmental gradients. She found that mid-elevation peaks of richness occur on mountains that have arid bases and higher precipitation at higher elevation. Mountains whose bases are wet and warm have no mid-elevation peak. Rather, richness declines monotonically with elevation, following the temperature gradient. Similarly, studying montane butterflies, Fleishman et al. (1998:2482) concluded that "environmental severity at either end and favorable conditions in the middle of the elevational gradient contributed to high species richness at intermediate elevations." Appendix C provides additional examples of MDE–environment collinearity on elevational gradients (Grytness and Vetaas 2002, McCain 2004, Carpenter 2005).

Collinearity in a river domain.—Dunn et al. (2006) recently noted higher riparian, non-ruderal, plant species richness in the mid-reaches of two Swedish rivers. They suggest that the mid-domain effect may help explain similar mid-course peaks of richness in other rivers, which have been little explored to date.

However, the Swedish results are mostly inconsistent with the hypothesized MDE. Non-ruderal species richness shows a mid-river peak (Dunn et al. 2006), but ruderal species richness increased monotonically downstream in the same rivers (Nilsson et al. 1989). Total species richness showed no significant relationship with position along the river (Nilsson et al. 1989). Although non-ruderal richness is correlated with the MDE prediction, the slope of the observed–predicted line differs significantly from the expected value $b = 1.0$ (Table 1).

As with other one-dimensional gradients, collinearity is very difficult to avoid in riverine studies. Many characteristics of rivers vary along the length of the river: temperature, light availability, current, disturbance, and so forth, sometimes in complex ways (Vannote et al. 1980).

Disentangling MDE–environment collinearity.—MDE predictions in two-dimensional domains are generally not collinear with environmental gradients because two-dimensional MDE models predict that richness should decline approximately radially from the mid-domain, whereas environmental factors rarely vary radially. Two-dimensional MDE models account for little variation in richness, and they typically find much poorer agreement along longitudinal transects than on latitudinal transects, in contrast to the MDE prediction (e.g., Jetz and Rahbek 2001, Ellison 2002, Hawkins and Diniz-Filho 2002: Fig. 2, Connolly et al. 2003, Kerr et al. 2006), except where collinearity was not avoided (Connolly et al. 2003, Bellwood et al. 2005).

Further, collinearity between environment and MDE predictions differs among geographic domains: Australia and Asia are warm and wet on one edge; Africa is warm and wet in the middle. Climate models derived in one domain make accurate predictions of richness in others (Currie and Paquin 1987, Francis and Currie 2003, Field et al. 2005, Kalmar and Currie 2007). If richness correlated with climate because of collinearity between environment and geometry, then climatic models should make poor predictions of richness in domains with different collinearity. The evidence is consistent with climatic controls on richness and not consistent with MDEs.

Finally, environment–MDE collinearity can be distinguished when environmental variables change. Richness tracks climate when environmental variables change (H-Acevedo and Currie 2003, White and Kerr 2006), even though geometry remains constant.

Spurious MDEs resulting from interpolation.—Madagascar has been presented as an "impressive victory" for the mid-domain hypothesis (Pimm and Brown 2004) precisely because the predictions of climatic and mid-domain hypotheses are not collinear in Madagascar. Climatic hypotheses predict highest richness in the North, nearest the equator, while the mid-domain hypothesis predicts maximum richness in the mid-latitudes of Madagascar. Lees et al. (1999) reported that several taxa do indeed have maximal richness in the mid-latitudes of the Madagascan rainforest biome.

However, the mid-domain peak in the Madagascan rainforest biome is equally consistent with a simple procedural artifact. Sampling intensity over Madagascar was very irregular (Lees et al. 1999), with a mid-domain peak. To compensate for irregular sampling, Lees et al. assumed range continuity: that each species was present at all latitudes between the northern- and southernmost observed presences. In their data set, 89.4% of species presences were inferred from interpolation. By definition, interpolation increases richness more frequently in the middle of a domain than at its edges. Grytnes and Vetaas (2002) argued that interpolation appeared to have contributed to a mid-domain richness peak that they observed in the Himalayas. In the Madagascan case, Lees et al. (1999:547) noted that "... the smoothed surfaces and parabolic trend shown by the interpolated data are reflected empirically [i.e., in the uninterpolated data] by only relatively few, better sampled grid-cells." Nonetheless, they concluded (p. 549) that, "Qualitatively at least, interpolation does not appear to alter the underlying trend shown by empirical results."

To test whether interpolation really does contribute little to observed mid-domain patterns in the Madagascan data, we carried out a simple simulation of the Madagascan data using a procedure similar to that of Grytnes and Vetaas (2002). We assumed that every Madagascan rainforest species is potentially present anywhere in the biome. A given species i has probability p_i of being observed in latitudinal band j within the Madagascan rain forest, and p_i is independent of position j on the latitudinal gradient. Species i may not be observed in band j because of neutral or meta-population processes, or simply due to insufficient sampling. We assumed that the distribution of p among species was log-normal, and we reduced the height of the distribution until we had a percentage of interpolated observations (85.2%) similar to that in the data of Lees et al. (1999) (89.45%). The simulated gradient of richness along the latitudinal transect without interpolation is flat, as expected (Fig. 5). With interpolation, a strong mid-domain peak emerges. This predicted pattern is virtually identical to the MDE prediction of Lees et al. ($r^2 = 0.99$). Observed richness is equally strongly related to both interpolation-predicted and MDE-predicted richness ($r^2 = 0.94$). Our interpolation-predicted pattern of richness is relatively insensitive to the frequency distribution of p_i when a high proportion of the observations are interpolated: a log-normal distribution of p_i and a flat distribution predicted very similar latitudinal gradients. Thus, the mid-domain peak of richness studied by Lees et al. (1999) in Madagascar plausibly reflects nothing more than the effect of interpolating sparsely sampled data across the mid-domain of the country.

Studies that use interpolated ranges also have the potential to inflate agreement with climatic hypotheses. Interpolation of ranges creates broad-scale spatial autocorrelation. MDE predictions and climate are both strongly spatially autocorrelated. This autocorrelation is likely to artificially increase correlations with other spatially autocorrelated variables. Recent simulation models by Storch et al. (2006) and Rahbek et al. (2007) show this nicely. These models postulate that species initiate colonization of continents as a function of environmental variables. Colonists' ranges then expand cohesively (i.e., in an autocorrelated manner) until they reach the range size of a real species. Predicted patterns of richness were compared to patterns obtained by superimposing range maps. Both studies found that the assumption of coherent ranges produced better agreement with observed richness patterns than did simple correlations between richness and climate. The reason is likely to be spatial autocorrelation: observed richness based upon interpolated range maps and the "spreading dye" simulated ranges are produced by similar processes. It may not be surprising that agreement between the two is good. The most obvious solution to the problem of interpolation is to choose a sufficiently coarse grain size in such a way that species' presences and absences can reliably be observed without interpolation.

Are MDEs in large- vs. small-ranged species evidence in support of the mid-domain hypothesis?

Mid-domain models predict strong mid-domain peaks of richness when species with broad ranges are considered, but much weaker peaks when an equal number of small-ranged species are considered. Several studies have observed this difference (Lees et al. 1999, Cardelús et al. 2006, Brehm et al. 2007) and infer support for the mid-domain hypothesis from it.

Spatial patterns of richness will always be stronger among large-ranged species than among small-ranged species, irrespective of the driving mechanism. Richness is the number of ranges that overlap in a given area. A given number of large ranges necessarily overlap more than the same number of small ranges, whether those ranges are distributed in a bounded domain or an unbounded one (e.g., the surface of a sphere). Consequently, mean richness per quadrat, and the variance in richness among quadrats, are necessarily smaller when small-ranged species are considered. This has often been observed empirically (e.g., Lennon et al. 2004: Fig. 2, Vázquez and Gaston 2004: Figs. 1 and 2, Rahbek et al. 2007: Fig. 1). As the variance of richness decreases, its expected correlation with any other variable decreases. This has also been observed empirically: richness of narrow-ranged species correlates less strongly with both environmental variables (e.g., Rahbek et al. 2007: Table 1) and with MDE predictions (Hawkins and Diniz-Filho 2002, Jetz and Rahbek 2002, Vetaas and Grytnes 2002) than the richness of large-ranged species does. Since weaker correlations for smaller-ranged species are expected irrespective of the hypothesis under study, this observation lends no support to any particular hypothesis.

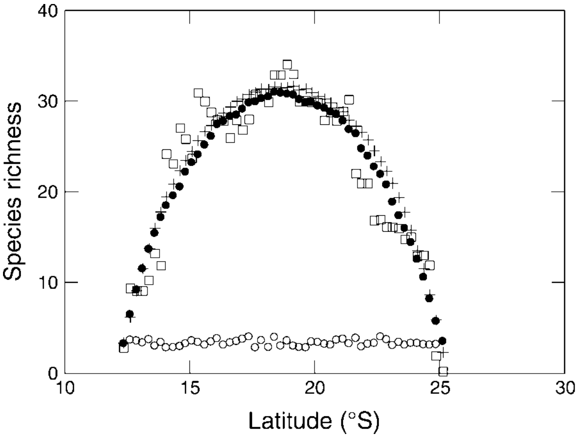

FIG. 5. A simulation of the latitudinal gradient in mycalesine (butterfly) species diversity in Madagascar. The observed pattern (□) and the mid-domain predicted pattern (+) are taken from Lees et al. (1999: Fig. 7). The remaining two patterns are predictions based on the following assumptions. First, assume that every species i can occur with a given probability p_i in each latitudinal band. The probabilities p_i are randomly drawn from a log-normal distribution. The expected richness gradient is flat (○). If ranges are assumed to be continuous, and absence between two presences is assumed to be an unobserved presence, then a mid-range peak of richness obtains (●), which is nearly identical to the predicted mid-domain peak. Thus, interpolation artifact is an equally powerful explanation of the latitudinal mid-domain peak in Lees' data.

The potential problems of using mid-domain models

The lack of agreement between observed and MDE-predicted patterns of richness has two possible interpretations. First, the mid-domain hypothesis may simply be incorrect: observed patterns of richness do not, in fact, necessarily include MDE-predicted patterns of richness. This could happen if one or more of the assumptions of the mid-domain model were false. Alternatively, lack of fit to MDE predictions could, in principle, reflect effects of environmental variables. However, the residuals from MDE predictions are nearly always strongly spatially structured. If environmental variables are responsible for these deviations from MDE predictions, then environment and geometry must virtually always be strongly collinear in very idiosyncratic ways. Consider, for example, Fig. 2c. A model that would eliminate the pattern in the residuals must hypothesize that richness varies as (at minimum) a fourth-degree polynomial function of environment along latitudinal gradients. Because there are longitudinal *minima* of richness gradients in the Americas, the model would also have to postulate even stronger effects of variables that vary longitudinally, but not latitudinally. We know of no literature that postulates, much less shows, the existence of such effects.

MDEs as null hypotheses.—Neither of these interpretations precludes using MDE(x, y) as a statistical null hypothesis, since the verity of statistical null hypotheses is not an empirical issue. Whether MDE(x, y) is a biologically meaningful null hypothesis is a different matter. The mid-domain hypothesis was proposed as the pattern that is necessarily present in observed richness patterns, irrespective of environmental gradients. If MDE(x, y) is *not* necessarily present in any given pattern of richness, then the reason to use it as a statistical null vanishes. Worse, using it (as in Eq. 1) will artificially create patterns of richness in the residuals (Fig. 2c). Subsequent analyses of environmental variables will statistically account for the MDE-induced artifacts in addition to environmental effects.

Use of MDE(x, y) as a contributing variable in multiple regressions.—Mid-domain theory precludes using the predictions of a MDE model in a multiple regression with a fitted parameter because the slope must be 1.0. We have shown above that requiring the slope to be 1.0 is inconsistent with observation and leads to nonsensical expected correlations. If mid-domain patterns actually existed, then there would be very little variance in richness attributable to anything else.

If one ignores all this and includes MDE predictions in multiple regressions anyway, then the omnipresent collinearity between environment and MDE predictions will inflate the variances of the estimates of regression coefficients associated with both the environmental variables and the MDE. In essence, inclusion of collinear MDE predictions and environmental variables each mask each other's effects. Worse, if MDE(x, y) is an incorrect model of the variation in richness, then its inclusion in a multiple regression will create both spatial pattern and autocorrelation in the residuals, since MDE(x, y) is spatially structured. Biological interpretation of such patterns would be perilous.

Conclusion

Broadscale patterns of species richness are not consistent with the predictions of the mid-domain hypothesis. Use of the mid-domain hypothesis as either a null hypothesis or as a contributing factor in explaining richness is inconsistent with mid-domain theory, and it risks creating important artifacts that would mislead further analyses. New models of geometric/spatial effects on richness are required.

It seems likely to us that spatial influences do exist. Range cohesiveness may generate spatial autocorrelation that resembles MDEs (Storch et al. 2006, Rahbek et al. 2007). Source–sink dynamics (Grytnes 2003*b*) or neutral processes (Rangel and Diniz-Filho 2005) may also produce geometric patterns. Evaluation of these hypotheses against observed patterns of richness may prove to be fruitful. It is also possible that MDEs may be more evident within biomes than in broader areas (Colwell et al. 2004), although this remains to be demonstrated. However, in our opinion, there is little point for future studies to continue to use a model whose predictions are so patently inconsistent with observed patterns of richness. There is no point whatever in showing that particular gradients show the weakest prediction of mid-domain theory—a mid-domain peak of richness—if those studies do not also test the stronger mid-domain predictions, as well as possibly collinear relationships with environmental variables.

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APPENDIX A

Sources of data and notes used in the compilation of Table 1 (*Ecological Archives* M078-001-A1).

APPENDIX B

Continental variation in richness and MDEs (*Ecological Archives* M078-001-A2).

APPENDIX C

Discussion of further examples of MDE predictions that are strongly collinear with environmental gradients (*Ecological Archives* M078-001-A3).