When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect

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ABSTRACT

Aim Recently, a flurry of studies have focused on the extent to which geographical patterns of diversity fit mid-domain effect (MDE) null models. While some studies find strong support for MDE null models, others find little. We test two hypotheses that might explain this variation among studies: small-ranged groups of species are less likely than large-ranged species to show mid-domain peaks in species richness, and mid-domain null model predictions are less robust for smaller spatial extents than for larger spatial extents.

Location We analyse data sets from elevational, riverine, continental and other domains from around the world.

Methods We use a combination of Spearman rank correlations and binomial tests to examine whether differences within and among studies and domains in the predictive power of MDE null models vary with spatial scale and range size.

Results Small-ranged groups of species are less likely to fit mid-domain predictions than large-ranged groups of species. At large spatial extents, diversity patterns of taxonomic groups with large mean range sizes fit MDE null model predictions better than did diversity patterns of groups with small mean range sizes. MDE predictions were more explanatory at larger spatial extents than at smaller extents. Diversity patterns at smaller spatial extents fit MDE predictions poorly across all range sizes. Thus, MDE predictions should be expected to explain patterns of species richness when ranges and the scale of analysis are both large.

Main conclusions Taken together, the support for these hypotheses offers a more sophisticated model of when MDE predictions should be expected to explain patterns of species richness, namely when ranges and the scale of analysis are both large. Thus the circumstances in which the MDE is important are finite and apparently predictable.

Keywords
Diversity gradients, elevation, latitude, mid-domain effect, range size, spatial extent.

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INTRODUCTION

Research effort in ecology and biogeography has long focused on identifying the environmental driver(s) underlying broad-scale patterns in species diversity (e.g. Forster, 1781; Hawkins *et al.*, 2003; Willig *et al.*, 2003). Despite decades of research, the rancour over the explanation for diversity patterns remains high, at least in part because in recent years many studies have found support for mid-domain effect (MDE) null models of diversity. These models predict the patterns of diversity expected in the absence of strong abiotic and biotic gradients on the distribution of species along domains (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Colwell *et al.*, 2004).

The mid-domain effect is the pattern that results from the random overlap in the distribution of species ranges along bounded domains (Colwell & Hurtt, 1994; Lees *et al.*, 1999; Colwell & Lees, 2000; Colwell *et al.*, 2004). Due to spatial constraints, more species are expected to overlap by chance near the centre of the domain than at the edges of the domain. In nearly all cases, the pattern produced by such mid-domain effect null models (and

hence the name of the models) is one in which ranges overlap in the middle of the domain and produce a hump-shaped pattern of diversity, much like empirical patterns seen along elevational gradients (Fleishman *et al.*, 1998; Kessler, 2001; Grytnes & Vetaas, 2002; Sanders, 2002; McCain, 2004a; Cardelús *et al.*, 2006; Watkins *et al.*, 2006), latitudinal gradients (Lees *et al.*, 1999; Colwell & Lees, 2000; Jetz & Rahbek, 2001; Koleff & Gaston, 2001; Ellison, 2002; Connolly *et al.*, 2003; McCain, 2003), temporal domains (Dunn *et al.*, in press), bathymetric depth gradients (Pineda & Caswell, 1998) and river courses (Dunn *et al.*, 2006).

In some cases, the variation in species diversity fits MDE predictions well, often better than all other measured variables (Fleishman *et al.*, 1998; Lees *et al.*, 1999; Jetz & Rahbek, 2001, 2002; Kessler, 2001; Ellison, 2002; Sanders, 2002; Connolly *et al.*, 2003; McCain, 2003; Romdal *et al.*, 2005; Cardelús *et al.*, 2006; Watkins *et al.*, 2006; Kluge *et al.*, 2006; Dunn *et al.*, 2006, in press). Yet in other cases, the MDE explains little to no variation in species diversity (Koleff & Gaston, 2001; Diniz-Filho *et al.*, 2002; Hawkins & Diniz-Filho, 2002; Laurie & Silander, 2002; Colwell *et al.*, 2004; McCain, 2005, 2006). Cases where empirical diversity patterns are well explained by null models are used as general support for their continued use (e.g. Sanders, 2002; McCain, 2003, 2004a; Colwell *et al.*, 2004). In contrast, cases where null models do not predict patterns of diversity are often levelled as general criticisms of MDE null models (Diniz-Filho *et al.*, 2002; Laurie & Silander, 2002; Zapata *et al.*, 2005). The discrepancy among studies in the fit of MDE null models seems to beg the question, why do some diversity gradients fit MDE predictions but others do not?

Based on an analytical model, Lees *et al.* (1999) hypothesized that MDE null models should have a higher explanatory power for large-ranged taxa than for small-ranged taxa. Large-ranged species are constrained to a relatively narrow array of possible positions by virtue of their range size. Results from individual studies or regions indicate that when species are split into large- and small-ranged groups, the diversity patterns of groups of large-ranged species are often better predicted by MDE null models than by environmental variables, whereas groups of species with small ranges on the same domains are poorly predicted by MDE null models (e.g. Jetz & Rahbek, 2002; Cardelús *et al.*, 2006). However, Lees *et al.*'s (1999) hypothesis has yet to be rigorously and empirically tested in comparisons among domains and taxa. If the hypothesis of Lees *et al.* (1999) is supported, variation among studies in the range size (relative to domain size) could potentially explain substantial variation among those studies in the fit of MDE null models.

As with many other factors that influence diversity patterns, such as productivity, rainfall and temperature (e.g. Whittaker *et al.*, 2001; Rahbek, 2005), the predictive power of the MDE may depend on spatial scale. Environmental variables, such as productivity and temperature, seem to do a better job in predicting patterns of diversity for smaller spatial extents (e.g. Rahbek, 2005). Conversely, it may also be along these smaller spatial extents that patterns of diversity deviate most from MDE null model predictions. The hypothesis that MDE null models explain more variation at larger than smaller spatial extents remains untested, both within and among studies.

We test two hypotheses in this paper: (1) small-ranged taxa are less likely to show mid-domain patterns of species richness, and (2) mid-domain patterns of species richness will be least apparent at small spatial extents. If these hypotheses are not rejected, they may explain differences among regions and studies in the extent to which patterns of species diversity fit predictions of MDE null models. We examine the explanatory power of the MDE for a wide range of taxonomic groups, spatial scales and domain types using 108 data sets varying from transects along elevational gradients to species distributions at continental scales.

METHODS

We compare the explanatory power of MDE null models among studies, regions and taxa, focusing on the explanatory power of range size (measured relative to domain size) and domain size (spatial extent). The underlying premise of the mid-domain effect is that spatial boundaries cause more overlap of species ranges towards the centre of an area where many large to medium-sized ranges must overlap but are less likely to abut an edge of the area (Colwell & Hurtt, 1994; Lees *et al.*, 1999; Colwell & Lees, 2000; Colwell *et al.*, 2004). MDE null models approximate the pattern of richness expected based on spatial constraints alone, were the empirical range mid-points of species to evolve at random with respect to the domain. To derive the distribution of diversity predicted by spatial constraints, a MDE null model program randomizes the placement of ranges (drawn from the empirical range size frequency distribution and hence maintaining the effects of the environment and history on range size) by choosing a particular empirical range size paired with a random mid-point drawn from a uniform distribution.

One way in which different one-dimensional MDE null models differ is in what happens when the model encounters a range and mid-point combination that extends beyond the domain. In one model (model 2, Colwell & Hurtt, 1994) such pairs are omitted and a new mid-point is drawn for that range size until the pair falls within the bounded area. Alternatively, in spreading dye null models, ranges are allowed to 'bleed' back into the domain the distance by which they extend beyond the domain (e.g. Jetz & Rahbek, 2002). Other models can be envisioned (e.g. Grytnes, 2003; Dunn *et al.*, 2006), but these have been the two primary models employed to date. Thus, the randomization procedure is constructed to determine the expected diversity pattern for an empirical range size distribution within a constrained space in the absence of the effects of environmental gradients on range placement, but while preserving the effects of environmental gradients and history on range size. Empirical diversity patterns can then be compared with MDE diversity predictions to determine whether diversity could be coincident with this constraint of space. Fits to the null model can then be detailed with linear regressions or other models of the relationship between empirical diversity and average MDE predicted diversity.

In addition to the differences among MDE null models in randomization algorithms, models can also differ in terms of the range size distributions used (see review in Colwell *et al.*, 2004). Some studies use theoretical range size frequency distributions

(RSFDs; Diniz-Filho *et al.*, 2002 in our analyses), but the majority use empirical range sizes (e.g. McCain, 2004a). Nonetheless, despite the differences among studies in the specifics of models, the general predictions are the same, a unimodal richness pattern with diversity peaking at the mid-point of the domain and declining monotonically towards the edges. For this work, all studies are based on MDE null models that use randomizations of empirical range sizes (e.g. RangeModel, Colwell, 2005; Mid-Domain Null, McCain, 2004b).

For our analyses, we extracted three pieces of information from each MDE null model dataset ($n = 108$): the *spatial extent* of each domain, the mean range size of the group of species relative to the size of the domain (hereafter range size:domain size ratio) and the coefficient of determination (r^2) for the regression of empirical diversity on predicted diversity of MDE null models. We focus on mean range size as an independent variable rather than some other measure of range size distributions because mean range size is easily extracted from published studies, whereas other measures of range distributions are not. We consider the merits of considering mean range size relative to other measures of range size in the discussion.

The four spatial extents into which studies were grouped were: (1) continental studies which considered entire contiguous landmasses (e.g. the Americas or Madagascar, but not North America), (2) regional studies which considered regions that defined either major ecological boundaries (e.g. biomes, or entire river systems) or geopolitical boundaries (e.g. Peru), (3) gamma (γ)-elevational studies that consider an entire mountain or mountain range, and (4) alpha (α)-elevational studies that consider a single elevational transect within a region. The different extents are not easily expressed in units, since the most appropriate unit of measurement differs among domains (e.g. metres above sea level for elevations, latitudinal degrees for continental gradients). Because extent is a continuous variable these groupings are imperfect, but the categories capture the magnitude of differences in extent necessary to understand its importance to the relationship between patterns of diversity and the MDE.

We compiled the data for this analysis from Colwell *et al.* (2004) and more recent studies of the MDE for 108 data sets which collectively represent work on many different taxa from the Americas, Africa, Asia and Europe (see Appendix S1 in Supplementary Material). This is by far the most comprehensive examination of when MDE null models succeed or fail, and the only statistical comparison. Studies varied in their particulars but were consistent in the definitions of range size and in most aspects of null model algorithms and statistical analyses (Appendix S1 in Supplementary Material). Because the use of r^2 values as an independent variable potentially violates some assumptions of traditional parametric analyses, we employed nonparametric Spearman rank correlation techniques to examine the relationship between r^2 values and range size:domain size ratios for each of the spatial extents separately. The dependent variable in the analyses was the coefficient of determination for regressions of empirical species diversity against null model predictions, and the independent variables were either the spatial scale of the region considered or the ratio of range size:domain size. In all among-study comparisons, we considered range size:domain size ratios in our analyses, rather than range size, since it is the size of the range relative to the domain, not in absolute terms, that is relevant to null model predictions.

In addition to the among-domain comparisons (as described above), we also compared the effect of range size within domains on the predictive power of the MDE. These analyses included either: (1) studies or groups of studies that considered multiple taxonomic groups from one domain (e.g. birds and mammals of Peru) or (2) split one taxonomic group into large- and small-ranged species and examined each size category separately. For each of these cases, we compared whether the smaller-ranged taxon or group on the domain showed a lower fit to MDE null model predictions than the larger-ranged taxon or group (see Appendix S2 in Supplementary Material). When more than two taxonomic groups were considered along the same domain, we used regression analyses where the coefficients of determination for the regression of species diversity on MDE null model predictions (estimated from original studies) were the dependent variables and the mean range size of the group of species considered was the independent variable. Significant positive relationships between range size and MDE null model coefficients of determination were then included in the binomial tests in the same way as pairwise comparisons showing the same pattern. We then used binomial tests (test proportion = 0.5) to test whether the proportion of studies showing higher coefficients of determination differed when large-ranged species were considered relative to when small-ranged species were considered. The binomial analysis of the effects of range size differs in terms of data and interpretation from the Spearman rank correlation analyses in two important ways. First, the binomial analysis minimizes the number of potentially confounding factors (i.e. those other than range size) since the comparisons are always for different groups within the same site. Second, whereas the data used in the Spearman rank correlation analyses are for entire taxa (e.g. birds), the binomial analysis also included comparisons within taxa. For example, comparisons of large-ranged and small-ranged birds on the same domain were included. In the binomial analyses, range size (rather than the ratio of range size to domain size) was used as the independent variable, since the domain is constant. Here, the analysis is not on the coefficient of determination *per se*. Rather, the binomial test is concerned with whether the relationship is positive or negative.

Similar to the analyses of range size within domains, we also compared the effects of spatial extent within regions for those studies or groups of studies that considered the same taxon at multiple scales within a region (see Appendix S3 in Supplementary Material). To test whether the effects of the range size:domain size ratio are independent of the spatial extent of analysis, we used binomial tests (test proportion = 0.5) to compare the proportion of cases in which the diversity pattern of a group of organisms was better explained at larger extents relative to smaller extents by MDE null models. Like the binomial test for the effects of range size, the binomial test for the effects of spatial extent controls for differences among domains to a greater extent than do the Spearman rank correlation comparisons among domains.

Table 1 Results of Spearman rank correlation for the effects of range size (relative to domain size) and spatial extent on coefficients of determination for MDE null model predictions

Analysis	*r*	*P*	*n*
Effects of range size on MDE *r*²			
All combined	0.282	0.0018	108
Continental	0.927	0.0027	12
Regional	0.655	0.0018	21
Gamma	0.202	0.1314	32
Alpha	0.238	0.0571	45
Gamma and alpha	0.214	0.314	77
Effects of spatial extent on MDE *r*²			
Scale	0.800	0.0823	4
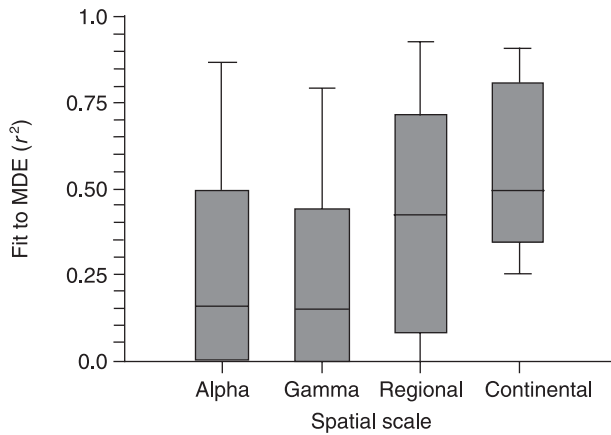
**Figure 1** Box plots indicating the explanatory power (r^2) of MDE null models at four spatial scales: α-elevational and γ-elevational studies, regional and continental. Regional and continental scale diversity data tend to fit the predictions of the MDE null models better than do the alpha and gamma diversity data. Lines within box plots indicate the median.

RESULTS

The explanatory power of MDE null model predictions (estimated by coefficients of determination r^2) was dependent on the range size:domain size ratio and the spatial extent of analysis (Table 1, Figs 1 & 2). When the spatial extent was large, MDE coefficients of determination were higher than when the spatial scale was small (Table 1, Figs 1 & 2); this relationship was strong ($r = 0.8$) but not quite significant due to the small number of scales included ($n = 4$). Range size explained most of the variation in the explanatory power of MDE predictions at large scales (continental $r = 0.927$, regional $r = 0.655$), but almost none of the variation at small scales (gamma $r = 0.202$, alpha $r = 0.248$) (Fig. 2).

When two taxonomic groups (e.g. birds and plants) or groups of species split by range size (into halves) from the same domain were examined, we found that the MDE explained more variation in diversity for groups with larger average range sizes than it
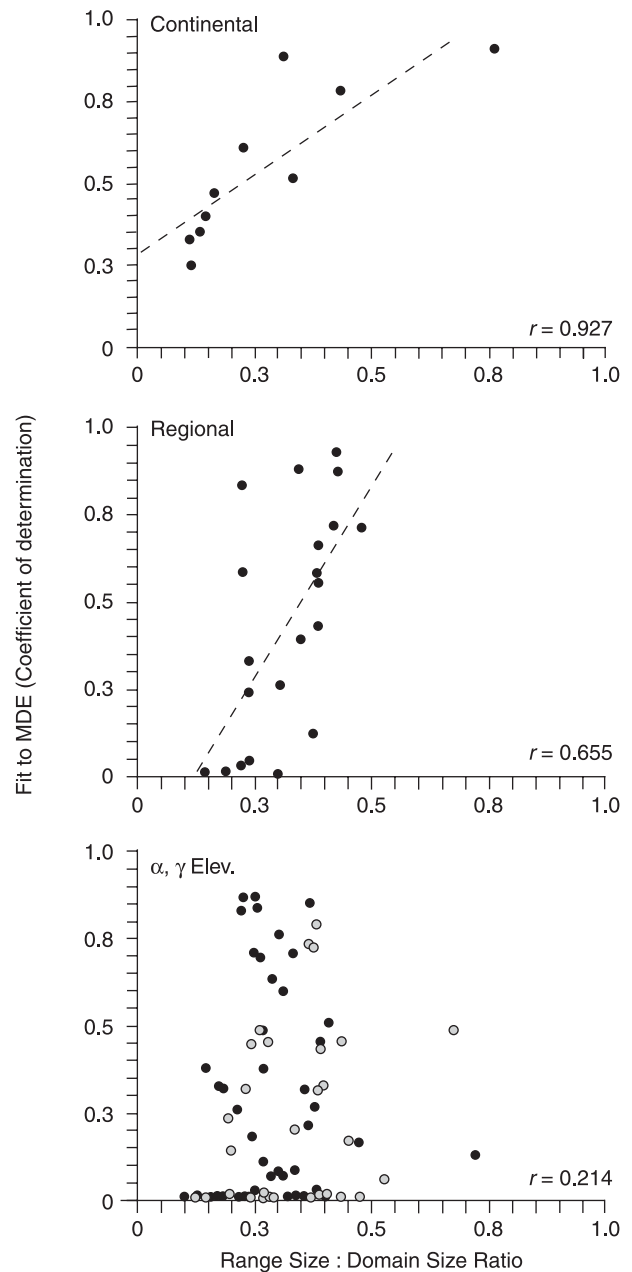
Figure 2 Scatterplots showing that at large spatial scales (regional and continental), the larger the ratio of average range size of a taxonomic group to domain size, the better the fit to predictions of the MDE null model, whereas the relationship does not exist at smaller spatial scales: alpha (black circles) and gamma (grey circles) elevational gradients. Dashed lines indicate directions of relationships, not statistical inference.

did for taxonomic groups with smaller average range sizes (20 of 24 cases; binomial, $P < 0.006$). Two of the four domains in which diversity in three or more taxonomic groups was measured, the Americas ($r^2 = 0.57$, $n = 7$, $P = 0.05$; Romdal *et al.*, 2005) and the Carrasco elevational transect in Bolivia (α-elevational, $r^2 = 0.78$, $n = 8$, $P = 0.004$; Kessler, 2001), showed a positive and significant ($P < 0.05$) relationship between MDE coefficients of determination

and average range size (see Appendix S2 in Supplementary Material). For the other two domains, Braulio Carillo in Costa Rica and the regional elevational gradient in Papua New Guinea, range size and MDE coefficients of determination were not correlated (Braullio Carillo, α-elevational, $r^2 = 0.32$, $n = 4$, $P = 0.4$; Papua New Guinea, regional, $r^2 = 0.482$, $n = 3$, $P = 0.51$). In eight of the nine cases where diversity patterns of the same taxon could be considered at multiple scales, diversity was better explained by the MDE null model at the larger rather than smaller spatial scale (binomial, $P = 0.039$; see Appendix S3 in Supplementary Material).

DISCUSSION

We have tested two hypotheses related to when mid-domain null models predict empirical patterns of species richness, namely that richness patterns of large-ranged groups of species should be more consistent with MDE predictions than those of small-ranged groups of species, and that MDE null models should explain more variation in richness at larger spatial extents than at small spatial extents. To our knowledge, this is the first attempt to discern a general pattern among studies with regard to when spatial variation in diversity fits MDE null models and when it does not. At least some of the debate around the value and importance of MDE null models is centred on whether or not empirical patterns of diversity do or do not support MDE null model predictions (e.g. Colwell *et al.*, 2004). While MDE null models predict empirical diversity patterns in many studies, they fail to do so in others. Our results show that much of the variation among studies in the predictive power of the MDE depends on the range sizes of species and the scale of analysis.

Hypothesis 1, null models and range size

Our analyses support a key prediction of MDE theory, namely that richness of large-ranged groups of species should be more consistent with MDE predictions than that of small-ranged groups of species, (e.g. Lees *et al.*, 1999). Overall, mean range size (measured as the ratio of mean range size to domain size) had a significant effect on the explanatory power of MDE among studies. In addition, when particular domains were considered for multiple taxa or groups of species, large-ranged groups of species were more likely (20 of 24 cases) to have diversity patterns that were better explained by MDE null models. As a more concrete example of the general pattern, in studies of latitudinal gradients in the Americas more than half of the variation among taxa (i.e. various bird taxa, marsupials and bats) in fit of the MDE to empirical patterns of diversity is explained by differences among taxa in terms of mean range size. Romdal *et al.* (2005) qualitatively reported on the same pattern in their analyses of these data sets, wherein the smallest-ranged taxon (hummingbirds) has ranges clustered in the middle of a domain to a greater extent than predicted by the null models, and the richness pattern of the largest-ranged taxon (raptors) is well predicted by the null models. The effect of range size on the fit of MDE null models was strongest at large spatial extents, and weak to absent at the smaller spatial extents (Fig. 1). Thus we find that for taxa with

large range sizes at larger spatial scales, patterns in the diversity of species have substantially better fits to MDE predictions. Our results empirically confirm the theoretical prediction of Lees *et al.* (1999) for the first time for comparisons among domains.

The conclusion that MDE null models have the highest predictive power for large-ranged species both within and among domains has several practical and theoretical implications. First, because the species of greatest conservation concern typically have small ranges, diversity patterns of those species are best considered in relation to factors other than MDE null models. As has been pointed out elsewhere (e.g. Jetz & Rahbek, 2001, 2002; Jetz *et al.*, 2005), it also means that studies that consider all species together without considering small-ranged species separately will often miss the species diversity patterns of the species of greatest concern because they are swamped by the mid-domain effects of large-ranged species. Second, our results also indicate that diversity patterns of some taxa and domains (those with small range sizes relative to domain size), as predicted by theory, are less likely to be strongly affected by mid-domain effects, and perhaps more likely to be driven by historical or environmental factors. Taxa with small average ranges may be the best test beds for examining the effects of history and the environment on diversity patterns (see also Jetz *et al.*, 2005). Ironically, the historical focus in studies of diversity has been on vertebrates and plants (e.g. all but 12 of those data sets included in this study), which may prove to have larger average ranges than do many groups of insects (e.g. Dunn, 2005), which might best show the signal of the factors of interest.

It is worth noting that we found a relationship between range size and explanatory power of the MDE null model despite the fact that we used a very simple measure of range size distribution, namely mean range size. We used mean range size because it is the measure of range size distributions most frequently available from studies of the MDE. However, two range size distributions with the same mean might have very different distributions. For example, imagine one distribution where every range is of average size and another where some ranges are large and many are small. As a consequence, range size distributions could actually explain more of the variation among studies and domains in MDE explanatory power than we show here.

Hypothesis 2, null models and scale

Our results supported the hypothesis that MDE null models have less predictive power for small domains. Independent of the range size:domain size ratio, MDE null models were poorer predictors of diversity at smaller spatial extents than at larger spatial extents. Range size (relative to the size of the domain) explained little variation in species diversity for α-elevational and γ-elevational studies (Fig. 2). Although the explanatory power of the MDE was high for some individual α- and γ-elevational studies (e.g. Kessler, 2001), on average, null models explained less than 25% of variation. Rahbek (2005) concluded that productivity and other environmental variables explain less variation in patterns of diversity at large spatial extents. The lack of a MDE trend

in small-scale studies may be due to a variety of factors. Coefficients of determination for α-elevational and γ-elevational level studies may be small because, for elevational gradients, climatic factors and area are strongly correlated with elevation (e.g. McCain, 2005, 2006), perhaps more so than is the case along, for example, latitudinal gradients (e.g. Rahbek, 2005). Further, favourable ecological conditions (e.g. temperature, rainfall) may diminish more quickly (in relation to size of domain) with elevation than with latitude.

A second possible explanation for the low explanatory power of MDE null models at small spatial extents is that as smaller and smaller spatial extents are considered, ranges are smaller relative to the size of the domain. This might be expected if, for example, particular climate regimes and hence habitat types (e.g. montane forest) occupy a smaller proportion of smaller gradients. However, at least for the analyses considered here, there was not a strong relationship between spatial extent and range size.

A final explanation for a link between spatial scale and the fit of MDE null models is that along continental domains (but not smaller domains) those environmental factors that drive patterns of diversity (e.g. temperature and productivity) peak in the middle of the domain. If this were generally true, MDE predictions might better explain empirical richness patterns at large scales simply as a consequence of covariation between MDE predictions and productivity. We suspect this is not the case for three reasons. First, productivity and favourable climate do not seem to be more likely to be drivers of richness patterns on the large-scale domains than on the smaller ones, more likely the reverse (e.g. Rahbek, 2005). Second, it is not obvious that the peaks in productivity or other environmental variables are more likely to be in the middle of larger spatial extents. The larger domains we considered included both regions where productivity and temperature do peak in the centre of the domain (e.g. Romdal *et al.*, 2005, the Americas) and examples where they do not (e.g. Lees *et al.*, 1999, Madagascar). Similarly, on some elevational gradients productivity peaks at the bottom of the gradient and in others productivity appears to peak closer to the middle of domains (Rahbek, 2005). Finally, in those large-scale analyses where environmental variables were explicitly incorporated into multivariate analyses, mid-domain null models remain significant predictors of diversity (Jetz & Rahbek, 2001, 2002).

The significance of the differences among spatial extents in the fit of MDE null models depends in part on the cause of the difference. If the difference among scales is due to differences in the relative importance of environmental and historical factors among different extents then there is no reason to expect that more sophisticated null models (e.g. Dunn *et al.*, in press) will yield better fits.

Conclusions

In sum, we have proposed a framework for understanding when the MDE does and, just as interestingly, does not predict patterns of diversity along bounded geographical domains: MDE null models consistently fail at predicting empirical diversity patterns for groups of small-ranged species and at small spatial extents. In contrast, MDE null models frequently predict variation in species diversity for groups of large-ranged species, particularly at large spatial scales.

Much of the debate regarding the use and abuse of MDE null models revolves around whether MDE null models fit the data. We suggest that there is little reason for continued debate about the role of MDE null models where ranges are small. Similarly, where domains are small the MDE may have a limited role. Thus, for the vast majority of cases in which diversity has been studied (most of which are on small domains), explanations other than mid-domain effects are necessary. Large domains on which species have large ranges are the context in which mid-domain null models are most important to consider. These big domains (the Americas, Africa, Madagascar, etc.) remain the focus of the most animated debates about mid-domain null models (e.g. Colwell *et al.*, 2004, 2005; Zapata *et al.*, 2005), and have the longest history of study (e.g. Forster, 1781). But because of the strong mid-domain effects at large scales, latitudinal gradient studies may tell us the least about the effects of history and environment on species diversity.

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BIOSKETCHES

Robert R. Dunn studies the ecology and evolution of ant-mediated plant dispersal in south-western Australia and patterns of diversity and ecological and evolutionary causes and consequences more generally. In his work on dispersal, he is interested in the linking of patterns of dispersal distance, range size and diversity to the evolution of dispersal mode.

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Nathan J. Sanders uses a combination of experimental and descriptive approaches to pursue research in the determinants of diversity and community organization of ants, the causes and consequences of biological invasions, and how biotic and environmental factors influence species diversity at local and regional scales.

Editor: Jack Lennon

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article.

Appendix S1 Data sets used in the analyses

Appendix S2 Relationship between range size:domain size ratio and the coefficients of determination

Appendix S3 Comparisons of correlation coefficients at different spatial scales

Appendix S4 Supplementary literature cited

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2006.00284.x

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