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E-Reply

The Mid-Domain Effect: There's a Baby in the Bathwater

Robert K. Colwell,[1,*] Carsten Rahbek,[2] and Nicholas J. Gotelli[3]

1. University of Connecticut, Storrs, Connecticut 06269;
2. Zoological Museum, University of Copenhagen,
Universitetsparken 15, DK-2100 Copenhagen, Denmark;
3. University of Vermont, Burlington, Vermont 05405

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In a recent article (Colwell et al. 2004; hereafter CRG), we reviewed all studies of the mid-domain effect (MDE) published up to that time and responded to earlier critiques of MDE by (among others) Hawkins and Diniz-Filho (2002) and Zapata et al. (2003). The discussion continues here with comments on our article by Hawkins, Diniz-Filho, and Weiss (2005; hereafter HDW) and by Zapata, Gaston, and Chown (2005; hereafter ZGC). In this article, we respond to HDW and ZGC.

Null models and null hypotheses. ZGC defend their view of MDE models as null hypotheses subject to falsification. In contrast, proponents of MDE theory have always held that richness patterns have multiple causes. For example, referring to the effect of geometric (boundary) constraints on geographic patterns of species richness, Colwell and Lees (2000, p. 79) stated that "the question is not whether geometry affects such patterns, but by how much." We view any assessment of the role of geometric constraints as a problem of estimating the magnitude of the contribution (if any) of MDE to richness patterns ("how much"). Just as with other candidate causes of richness patterns (e.g., climatic, topographic, or historical drivers), the appropriate null hypothesis (if any) is that MDE makes no contribution to richness patterns, not that MDE uniquely and fully accounts for richness patterns. It is for this reason that we distinguish between MDE as a model and the hypotheses that can be framed regarding its predictions.

Ecologists, statisticians, and philosophers are currently debating the merits of formal hypothesis testing (Taper and Lele 2004), and there is a movement toward Bayesian (Ellison 2004) and likelihood (Hilborn and Mangel 1997) approaches to comparing model predictions with data. These newer approaches are consistent with our rejection of "all or none" evaluations of MDE and are concordant with our pluralistic view of the multiple forces that may be affecting species richness gradients.

Contrary to the claims of HDW and ZGC, MDE models are perfectly valid null models for species richness gradients that conform fully to the formal definition of a null model proposed by Gotelli and Graves (1996, pp. 3–4):

> A null model is a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution. The null model is designed with respect to some ecological or evolutionary process of interest. Certain elements of the data are held constant, and others are allowed to vary stochastically to create new assemblage patterns. The randomization is designed to produce a pattern that would be expected in the absence of a particular mechanism.

Classic MDE models hold constant the size of the domain, the range size frequency distribution (RSFD), the number of species in the domain, and the cohesion of each species' geographic range. As we explained in CRG, it is statistically more appropriate to resample ranges at random from the empirical RSFD than from any theoretical RSFD. The shape (in two-dimensional models) and placement of geographic ranges within the domain are allowed to vary stochastically. The models produce spatial patterns of species richness that would be expected in the absence of any direct effects of gradients in environment or history on richness patterns, although such gradients may nonetheless influence the RSFD (fig. 1, discussed later in more detail).

ZGC suggest (p. E145) that we (CRG) confuse "criticism of MDE models with criticism of null models in general." Although we wrote (CRG, p. E1) that "some criticisms of MDE apparently arise from misunderstandings of the nature of null models or of MDE models in particular," a contention that we defend above, nowhere did we suggest

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[*] Corresponding author; e-mail: colwell@uconn.edu.

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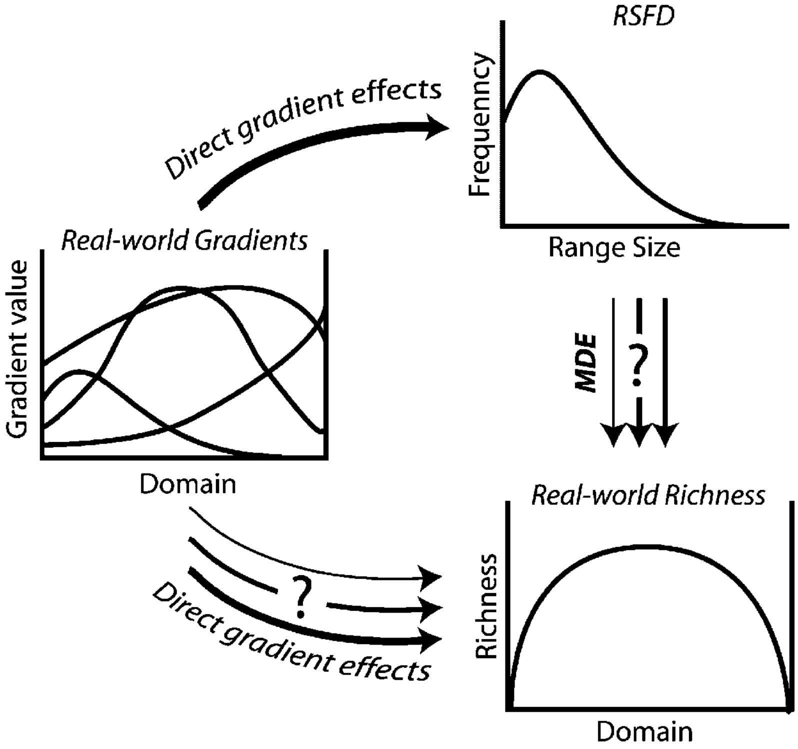

Figure 1: Causal paths between environmental gradients, the range size frequency distribution (RSFD), and patterns of species richness for a hypothetical, real-world domain. No one doubts that gradients directly affect the processes that determine the RSFD (*bold upper arrow*). The relative impact of direct gradient effects (*lower set of arrows*) and stochastic effects of boundary constraints (mid-domain effect [MDE], *vertical set of arrows*) on richness pattern is more variable, as indicated by the varying arrow widths and the question marks. Published studies indicate mixed causality, with the relative explanatory power of MDE dependent on range size, domain size, domain type, and taxon.

that ZGC or other cited critics oppose the construction and use of null models in general.

Ranges, Domains, and Environmental Gradients

MDE models ignore any known or suspected environmental gradients in the real-world domain, placing ranges *as if* there were no gradients within the domain (not "*when there are* no … gradients within the domain," as HDW claim; emphasis added). Or, as Connolly (2005, p. 1) put it, classic MDE models assume that "environmental conditions vary but that species' responses to environmental conditions would be sufficiently individualistic that, in the aggregate, no part of the domain would be more hospitable to species than any other part."

Both HDW and ZGC elaborate on their previous concerns (Diniz-Filho et al. 2002; Hawkins and Diniz-Filho 2002; Hawkins et al. 2003; Zapata et al. 2003) regarding what they view as a critical inconsistency in this approach. As ZGC put it (p. E145), if MDE models "assume an absence of environmental gradients, then the question is raised as to why all species are not distributed throughout the domain." Or, in HDW's words (p. E141), "how can we assume the existence of an RSFD in the absence of spatial and temporal environmental variation?"

This seeming paradox is resolved as follows. First, in the real world, populations (and thus ranges) are routinely shaped and limited by environmental factors, historical effects, and dispersal limitation. All parties agree that real-world RSFDs are the product of these forces (fig. 1, *arrow from gradients to RSFD*). HDW's suggestion that MDE models or MDE modelers assume that any real-world domain is free of environmental gradients mistakes a null model scenario for a statement about the real world. MDE models ask what richness patterns would look like if real-world environmental gradients within the domain had no direct effect on spatial patterns of species richness. Second, in classic MDE models, a mid-domain richness peak arises from the random placement of ranges sampled from any RSFD that includes ranges of at least moderate size in relation to the size of the domain. The shape and magnitude of the modeled richness peak depends entirely on the size and shape of the domain, the RSFD, and (to a lesser degree) the algorithm or model used for range placement (Connolly 2005). HDW and ZGC both express agreement with this mathematical proposition. In figure 1, the downward-pointing set of arrows, from RSFD to richness, indicates the potential influence of this fundamental MDE mechanism on real-world richness patterns. Third, the MDE models criticized by HDW and ZGC randomize the placement of real-world ranges on the domain and then examine the spatial pattern of richness produced and compare it with the corresponding real-world richness pattern. The question posed by this procedure is to what degree real-world richness patterns may be distinguished from patterns driven by stochastic processes constrained by domain boundaries. Finally, environmental gradients in the real-world domain are explicitly ignored for the purposes of random placement of ranges in classic MDE models. But in the most complete studies (e.g., Jetz and Rahbek 2002; Cardelús et al. 2005), real-world environmental gradients are considered statistically in a multivariate context, together with MDE predictions, to evaluate direct effects of gradients on richness patterns (fig. 1, *arrows from gradients to richness*) versus the indirect effects of gradients expressed through the RSFD and range placement under geometric constraints (*vertical arrows*).

Figure 1 answers HDW's question, "what ecological and evolutionary factors are excluded from the null model?" Classic MDE models exclude the direct effects of environmental gradients on species richness, by setting to zero the set of arrows pointing directly from gradients to richness, for the sole purpose of developing MDE predictions. In the long run, process-based models (e.g., Connolly 2005; Davies et al. 2005; Rangel and Diniz-Filho 2005*a*) that mechanistically integrate geometric constraints with environmental gradients and/or evolutionary processes in bounded domains offer a way forward from the correlative approaches of both classic MDE analyses and conventional, regression-based analyses of richness in relation to environmental variables.

There are precise and widely accepted precedents for this approach in the extensive literature on null models for patterns of species co-occurrence (e.g., Gotelli 2000; Miklos and Podani 2004), niche overlap (Sale 1974; Winemiller and Pianka 1990), and phenological patterns (Poole and Rathcke 1979; Armbruster 1986; Morales et al. 2004). In each of these cases, it is routine to hold constant the distribution of empirical range sizes (number of occurrences, breadth of resource use, and flowering or fruiting period, respectively) of each species while randomizing the placement of those ranges within a specified domain (among islands, among resources, or across a flowering or fruiting season, respectively). In fact, as pointed out by Colwell and Lees (2000), MacArthur's and Pielou's "niche overlap" (null) models are even mathematically identical to simple MDE models. Co-occurrence models do not assume that the number of islands occupied by each species arises in the absence of dispersal history, niche overlap null models do not assume that niches evolve in the absence of environmental or resource patterns, and phenological null models do not assume that flowering or fruiting peaks evolve in the absence of seasons. Like MDE models, these classic null models are randomizations that are, by design, constrained by carefully chosen elements of real-world data.

Although MDE models show that, given a realistic RSFD, mid-domain richness peaks arise even when gradients are absent from the model domain (Connolly 2005), they neither assume nor demonstrate that such peaks appear only if gradients are absent. This point is strikingly illustrated by the work of Rangel and Diniz-Filho (2005*a*, not cited by HDW), whose process-based "evolutionary" models examine species richness on simple environmental gradients. These spatially explicit, stochastic models set up a monotonic environmental "suitability" gradient in a bounded domain, with the "best" environment at one end of the domain, where species establishment is favored. Each species is limited in its range by an interaction between steepness of the gradient and stochastically assigned, species-specific, environmental tolerance (following Kirkpatric and Barton 1997), yielding realistic RSFDs. (This aspect of the model corresponds precisely to the arrow from gradients to RSFD in fig. 1.) The conventional prediction—that the peak of richness will appear at the "good" end of the domain after a period of random speciation and extinction—is realized only when the environmental gradient is very strong, forcing species to have small ranges, given their environmental tolerances. With weaker gradients, ranges are larger, given the same tolerances, and a richness hump appears toward the "good" end of the gradient. In model runs with increasingly weakened gradients, the hump shifts toward the center of the domain. This happens because, under conditions of a weak gradient, ranges are the largest and overlap the most, and geometric constraints are least in conflict with the "suitability" gradient in regard to range placement. (In terms of the causal arrows in fig. 1, as gradients weaken, MDE becomes stronger relative to direct effects of gradients on richness patterns.) In these models, in which both RSFD and range placement are generated dynamically, even extremely weak environmental gradients can generate a realistic RSFD and a classic MDE. In Rangel and Diniz-Filho's models, the mid-domain peak disappears entirely only at precisely zero gradient strength. Similar results emerge from Connolly's (2005) process-based analytical models that explore how geometric constraints affect richness patterns on symmetric gradients.

In short, even in Rangel and Diniz-Filho's process-based models, the concern of HDW and ZGC regarding MDE and the assumption of no gradients ("how can we assume the existence of an RSFD in the absence of spatial and temporal environmental variation?") is a potential issue only at the theoretical but unrealistic limit of absolutely no gradients at all. The Rangel and Diniz-Filho models demonstrate elegantly not only all three causal relationships in figure 1 but also the shifting balance between direct effects of environmental gradients and RSFD-driven mid-domain effects.

Domain limits. ZGC (p. E145) seriously misrepresent our views on defining domain limits for MDE studies by claiming that we (CRG) argued that "there should be no distinction between hard and soft boundaries and that all domains should be biologically delimited by the distribution of the clade under study." We said no such thing. This false claim is completely at odds with our explicit endorsement of defining domains based on classical biogeographical units such as biomes, floristic or faunistic provinces, islands, continents, ocean basins, and full elevational transects, whether or not the clade (or taxonomically defined biota) under study fully occupies the domain, thus defined.

We pointed out a fundamental similarity between hard boundaries (e.g., shorelines for terrestrial and marine organisms) and soft boundaries (e.g., thermal tolerance limits): that both are ultimately defined by the adaptations of organisms. But the intent of that comparison was not to urge abandoning the use of classical biogeographic units, where they make sense. Instead, we were advocating the designation of domains based on other (adaptive) criteria, where classical biogeographic units do not make sense. For example, the northern and southern climatic limits for palms, which cannot survive ground frost, cut across numerous temperate biomes and ecoregions (Greenwood and Wing 1995). We agree with ZGC that there is an element of circularity in defining a domain in terms of the organisms that occupy it (although the same circularity exists in defining virtually all classical biogeographic units). Nonetheless, even if a domain is defined as the spatial union of all ranges under study for a particular MDE analysis, there is no reason to routinely expect a mid-domain peak in species richness in such a domain under traditional ecological assumptions, whereas MDE models predict such a peak. (Colwell and Lees [2000] outline how a dynamic evolutionary model might produce such a peak for the members of a clade, and Davies et al. [2005] explore the behavior of such a model.)

ZGC correctly point out that a literal interpretation of our discussion of domains based strictly on clades would require including marine mammals (and therefore oceans) in a study of focused on terrestrial mammals. For such cases, it would be better (following Colwell and Lees 2000, p. 75), to speak of "taxonomically defined biotas" instead of clades.

In summary, we agree with ZGC that domain definition is sometimes difficult and can be somewhat arbitrary. We do not agree that this methodological challenge means either that MDE cannot or should not be studied or that it does not contribute to patterns of species richness.

Model predictions and statistical assessment. ZGC take us to task for suggesting that they assessed MDE studies "from an 'all or nothing' viewpoint" in Zapata et al. (2003, pp. 684–688). It is true that the cited pages of Zapata et al. (2003) detail a careful analysis of statistical support for MDE studies, but that analysis seems contradicted by the overall conclusion of Zapata et al. (2003, p. 677) that "the models do not adequately describe observed species richness gradients and thus fail to explain them." This statement seems in full accord with ZGC's endorsement of uniformly applying the principle of falsification to MDE models rather than viewing them as a means to assess the contributions of stochastic processes to richness patterns in the context of mixed causality.

In discussing statistical assessment of MDE predictions in relation to real-world richness patterns, ZGC state, "As we and others have pointed out, a high coefficient of determination (R^2) could still mean a marked mismatch of species richness values. This point seems to have been missed by CRG." Not only did we not miss this point, but also we stressed it. We wrote (CRG, p. E13), "The correlation coefficient reflects the fit of the data to the MDE predictions in terms of relative, not absolute, magnitude. … An alternative approach is to examine the slope and intercept of the relationship between predicted and empirical richness," an approach suggested later in the same paragraph by ZGC, as if we had neglected it.

We readily agree with ZGC that "if MDE models had predicted a pattern of richness entirely at odds with that observed, they would never have been proposed as a general explanation for patterns of species richness." But we fail to see how that is an indictment of these models. The same criticism could be leveled at the heliocentric model of the solar system and most other models of natural patterns.

A more substantial criticism of the testing of MDE models is ZGC's contention that if MDE is driving richness patterns, then the fine structure of real-world patterns of range placement within real-world domains should match the fine structure of range placement in MDE model predictions. This issue was raised by Koleff and Gaston (2001), who compared beta diversity (species turnover) patterns for real-world data and the corresponding predicted spatial patterns from MDE models, and by Laurie and Silander (2002) and Connolly et al. (2003), who compared the pattern of range/midpoint plots with stochastic expectations. ZGC (p. E146) write, "If the models do not predict such patterns, then how well they predict patterns of species richness is irrelevant, as they cannot be capturing the processes determining the patterns of richness."

The approach is a valid one, but a closer look at the predictions of MDE models suggests that the match between empirical and modeled patterns of turnover should not be expected to be as strong as the fit of empirical total richness to modeled total richness, even in real-world data sets for which richness is strongly shaped by geometric constraints. Species with larger ranges disproportionately drive geographic patterns of richness because each is counted repeatedly over wide expanses of map area, whereas species with small ranges are counted over a limited area (Jetz and Rahbek 2001, 2002; Lennon et al. 2004). In contrast, measures of turnover or beta diversity are equally sensitive to the spatial distribution of endpoints for ranges of all sizes. A strong theoretical prediction of MDE models, repeatedly confirmed for empirical data (as summarized by CRG; see also Cardelús et al. 2005; Mora and Robertson 2005), is that larger ranges are more constrained by geometry than are smaller ranges. As range size increases from 0 toward the size of the domain, the scope for midpoint placement (the width of the constraint triangle in fig. 2 of Colwell and Hurtt [1994]) decreases linearly from the size of the domain to 0. For this reason, in a bounded, real-world domain, the influence of environmental or historical factors on range location is expected to be greater for smaller ranges than for larger ranges. Simple MDE models, on the other hand, which assume an absence of environmental drivers, predict, on average, a uniform plateau of richness for small ranges (Colwell and Hurtt 1994). Thus, the idiosyncratic, real-world richness patterns of small-ranged species tend to produce idiosyncratic patterns of turnover, even for data sets in which real-world patterns of species richness, driven by large-ranged species, are well predicted by MDE models. We conjecture that a comparison of species turnover patterns (and species midpoint patterns; see Connolly 2005) for large-ranged versus small-ranged species in such cases will routinely show that the former correspond better to model predictions than the latter.

ZGC (p. E147) contend that we all too readily accept "model fit" as "evidence of causality," whereas climate-based theories of species richness patterns have generated "a large body of tests of model fit but have also tested a wide range of assumptions and secondary predictions of these hypotheses." The most recent evaluation of many of those predictions (Currie et al. 2004) indicates that gradient-based theories of species richness still have far to go, and the same may be said for historical approaches to the problem (Wiens and Donoghue 2004), even though both approaches represent the accumulated wisdom of 125 years of thought and study. Of course, ZGC are right that identifying causality requires a deeper understanding of mechanism than simple, pattern-based MDE models can possibly offer, but "model fit" is nonetheless a reasonable early criterion in the development of any model. MDE theory is only a decade old, represents a fundamentally new framework for understanding patterns of species richness, and poses practical challenges for real-world tests, but it has already begun to change the way geographical patterns of species richness (and other bounded phenomena) are modeled and interpreted. Since the publication of CRG, recent articles have taken MDE in fruitful new directions (Bachman et al. 2004; Jetz et al. 2004; Morales et al. 2004; Rodriguez and Arita 2004; Arita 2005; Cardelús et al. 2005; Connolly 2005; Davies et al. 2005; Hernández et al. 2005; Herzog et al. 2005; Lusk et al. 2005; Mora and Robertson 2005; Rangel and Diniz-Filho 2005*a*, 2005*b*; Romdal et al. 2005).

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