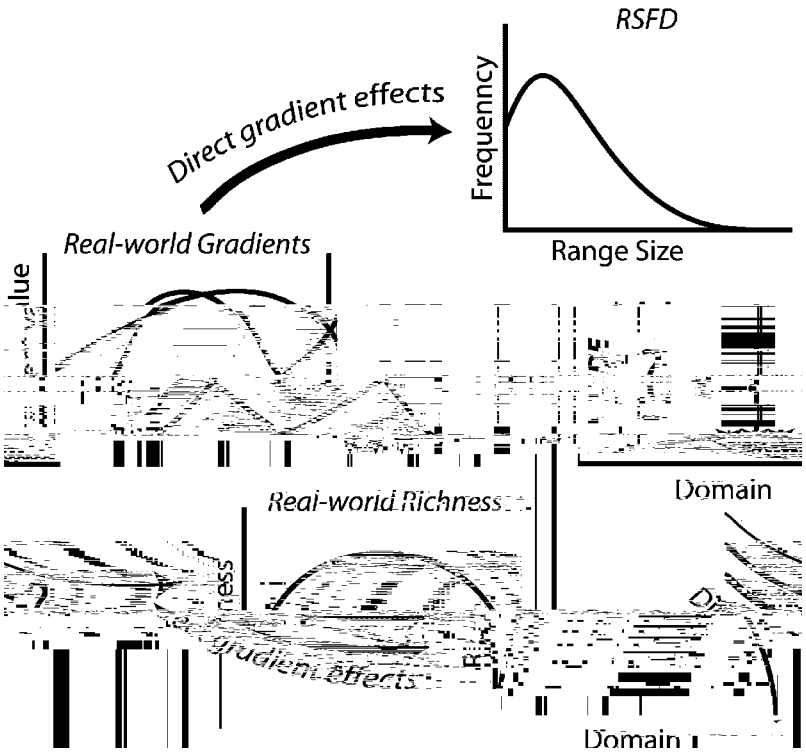


Figure 1: Causal paths between environmental gradients, the range size frequency distribution (RSFD), and patterns of species richness for a hypothetical, real-world domain. No one doubts that gradients directly affect the processes that determine the RSFD (*b d e a* ). The relative impact of direct gradient effects ( *e e f a* ) and stochastic effects of boundary constraints (mid-domain effect [MDE], *e ica e f a* ) 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 *a if* there were no gradients within the domain (not " *he he e a e* 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, *a f g adie 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

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 pr

In short, even in Rangel

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