

The Mid-Domain Effect and Diversity Gradients: Is There Anything to Learn?

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ABSTRACT: The mid-domain effect (MDE) has been proposed as a null model for diversity gradients and an explanation for observed patterns. Here we respond to a recent defense of the concept, explaining that it cannot represent a viable model in either real or null worlds. First, the MDE misrepresents the nature of species ranges. There is also an internal logical inconsistency underlying the MDE because the range size frequency distribution, necessary to generate a hump-shaped pattern under randomization, cannot exist in the absence of environmental gradients and is generated by the ecological and historical processes that the MDE claims to exclude.

Keywords: geographic ranges, geometric constraints, mid-domain effect, null models, diversity gradients, species richness.

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 ... designed with respect to some ecological or evolutionary process of interest” (Gotelli and Graves 1996, p. 3; see also Gotelli 2001). Despite their sometimes controversial history, null models are now widely used in different areas of ecological and evolutionary research. In this context, the mid-domain effect (MDE) has attracted much attention following its development by Colwell and Hurtt (1994), with the further formalization by Willig and Lyons (1998) and especially by Colwell and Lees (2000). Colwell et al. (2004) recently

reviewed the MDE in an effort to refute a wide range of criticisms to the idea, primarily raised by Hawkins and Diniz-Filho (2002), Laurie and Silander (2002), and Zapata et al. (2003).

The MDE proposes that “based on both simulations and analytical null models, it is now clear that a mid-domain peak or plateau in species richness is inevitable for virtually any set of ranges, theoretically or empirically, when these ranges are randomly placed within a bounded geographic domain, in the complete absence of any superposition of environmental gradients within the domain” (Colwell and Lees 2000, p. 70). Thus, proponents consider the MDE a null model that explains how diversity will be distributed in space when there are no environmental gradients within the domain. In other words, the MDE is a null model that generates a pattern in geographic space characterized by peaks of species richness in the middle of a domain, apparently generated by the random overlap of geographic ranges (the underlying process). We do not dispute that the basic patterns predicted by some MDE models are consistent with some observations. Ecologists have long been aware that many ecological phenomena reach their maximum expression at or near the middle of some range or gradient. Species abundances are often highest near the center of their range, local communities often support the most species at intermediate points in productivity or disturbance gradients, and species diversity usually reaches its maximum near the equator rather than at the poles. Thus, it is not surprising that studies often report patterns consistent with the general predictions of the MDE (Colwell et al. 2004). The critical question is not whether these patterns occur but why they occur and whether the MDE actually is a null model to contrast against biological or ecological processes.

If the MDE represents a valid null model and is confirmed in empirical data sets, a large set of the most interesting and important ecological and evolutionary patterns would have been explained as being largely independent of ecological or evolutionary processes, in sharp contrast to the results of more than 150 years of research. Not surprisingly, some ecologists disagree and

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have argued that the MDE does not represent a meaningful explanation for geographic diversity gradients (Hawkins and Diniz-Filho 2002; Laurie and Silander 2002; Zapata et al. 2003). However, as indicated by Colwell et al. (2004) and others (e.g., Pimm and Brown 2004), the criticisms have not been accepted, so we further develop these arguments here. Our primary criticism is that the MDE misrepresents the nature of species ranges and consequently fails to provide a null expectation in the absence of environmental gradients. Specifically, there is an inconsistency underlying the MDE concept because the range size frequency distribution (RSFD) necessary to generate hump-shaped patterns under the MDE null process cannot exist in the absence of environmental gradients and is in fact generated by the same complex ecological and evolutionary processes the MDE claims to exclude as a null model.

The Nature of Species Ranges

Using an approach in which observed geographical ranges are treated as innate objects and are reshuffled in space, it is possible to generate an MDE pattern when a geographic RSFD exists, whether the RSFD is generated deterministically or stochastically. There is no disagreement about this because it can be demonstrated mathematically and generated empirically by simulation models. With respect to using an RSFD to generate the predictions of an MDE model, Colwell et al. (2004, p. E7) proposed using observed RSFDs of a taxonomic group as surrogates that can incorporate into the model the “taxon-specific biological characteristics that are logically independent of spatial patterns of richness within the domain. Among other things, vagility, body size, population density, and evolutionary potential for speciation and extinction.” But few if any of these traits are indeed independent of spatial patterns, and the critical question becomes, How can we assume the existence of an RSFD in the absence of spatial and temporal environmental variation?

It is recognized by all ecologists that the environment, and its underlying dynamical forces acting over species' physiological tolerances, plays an important role in geographic range sizes. For example, if ranges existed independently of the environment, there would be no need to worry about the effects of climate change on biodiversity (see, e.g., Peterson et al. 2002; Thomas et al. 2004), nor could ranges be predicted using climatic and other environmental variables (bioclimatic envelopes; e.g., Peterson 2001; Scott et al. 2002; Pearson and Dawson 2003). Obviously, a geographic range size distribution is not independent of environmental effects but is, in fact, one consequence of the interactions between organism traits and environmental gradients. It is also worth noting that do-

main are themselves defined by environmental gradients, for example, sharp moisture gradients at coastlines and strong temperature gradients at mountain ranges, indicating that the models assume that environmental gradients occur only at the edges of domains and not in their interiors. There is no place on Earth where this assumption is valid at any spatial scale relevant to understanding species distributions. That is, all observed ranges of species on this planet are embedded within environmental gradients, and all observed RSFDs reflect that fact.

So, the interaction between organisms and environments leads to an internal inconsistency in the assumptions of the MDE; that is, if there are no environmental gradients within the domain, species could occur anywhere and everywhere, there could be no RSFD (ranges would be constant and as large as the domain), and, consequently, no MDE would exist. Also, if the MDE depends on the RSFD, which in turn is the result of multiple processes through time, what ecological and evolutionary factors are excluded from the null model? Although we agree that an RSFD can be viewed as a statistical aggregate for descriptive purposes, it is extremely difficult to partition the complex ecological and historical processes underlying this aggregate because in ecology and evolutionary biology, multiple processes acting simultaneously can lead to the same pattern. It is widely appreciated that pattern does not identify process, and the problem with the MDE is precisely that the self-same patterns of geographic ranges (i.e., the RSFD) that are generated by complex processes are used to propose an explanation for the spatial variation in diversity when these processes are claimed to be absent.

An Alternative Approach to Null Models for Diversity Gradients

As pointed out by Darlington (1957), geographic ranges have no physical existence. Rather, ranges represent an emergent property derived from aggregations of individuals so that the “real units of geographic ranges are the complex spatial and temporal patterns in which individual organisms are dispersed over the Earth” (Brown et al. 1996, p. 599). So, although in most macroecological studies geographic ranges are analyzed as coherent structures by measuring their size and shape, it is important to remember that this apparent structure is defined by the interactions between population dynamics and tolerance to environmental conditions. Forgetting this may result in misleading interpretations if one wishes to evaluate how these complex ecological processes influence the existence of the range. We believe that to understand patterns of diversity in a spatial context, it is better to construct models at the appropriate hierarchical level to understand true null expectations (i.e., the distribution of individuals in the ab-

sence of environmental gradients). The links among hierarchical levels and the convergence of predictions by models constructed at different levels have been investigated by several authors in other contexts (e.g., Blackburn and Gaston 2001; Gaston and He 2002; Watkinson et al. 2003). As we have already pointed out, with respect to geographic diversity gradients, the focal problem is how geographic range size is limited, permitting the existence of an RSFD in a constant environment. This directs us to the population dynamics models for the statistical distribution of range sizes and range boundaries that have been widely investigated in recent years (for reviews, see Brown et al. 1996; Butlin et al. 2003).

Even assuming that species can have intrinsically historical components creating variation among demographic rates and other life-history traits that could act independently of current environmental gradients, population growth models predict the eventual occupation of the entire domain (Renshaw 1991; Gaston and He 2002). Rates of range expansion will necessarily be related to the average distance moved by individuals from birth to reproduction, but given enough time, the population will expand to the boundaries of the domain. The speed of many biological invasions clearly indicates that the time needed for these full-range expansions is very short relative to the time necessary for the evolutionary origins of a biota. Of course, rates of range expansion need to be linked to the evolution of dispersal abilities; as recently pointed out by Holt (2003), after an invasion, a species may remain geographically stable (without shifts in range size) until genetic variants allowing long-term dispersal appear. Even so, the prediction of these models is a flat diversity gradient in which every species occurs everywhere.

Evolutionary models of geographic range size are frequently genetic-demographic tension models based on the interaction of gene flow and adaptation creating range boundaries (Kirkpatrick and Barton 1997; Butlin et al. 2003), arising from the pioneering work by MacArthur (1972). Building on the concept of central-peripheral populations popularized by Ernst Mayr on the early 1960s (see also Maurer and Taper 2002), Kirkpatrick and Barton (1997) proposed a model in which gene flow from the center of a range can constrain adaptation at the periphery and prevent the species from expanding indefinitely outward (via adaptation to increasingly different environmental conditions; for other demographic models of source-sink populations in which asymmetrical gene flow can inhibit local adaptation, see also Holt and Gaines 1992; Holt and Gomulkiewicz 1997). The details of Kirkpatrick and Barton's (1997) model are complex, but all situations can be described in terms of two aggregate parameters, A and B . The parameter A can be interpreted as the genetic potential for adaptation to the local ecological conditions,

whereas B is proportional to the speed with which ecological conditions change as one crosses the range and to the dispersal rate. If $B = 0$, reflecting no gradient and a constant environment, the ranges will be unlimited (see also Butlin et al. 2003). Colwell et al. (2004) suggested that gradient models, such as the one developed by Kirkpatrick and Barton (1997), could be used to evaluate the MDE. However, these models are not appropriate because gradient models do not predict an RSFD in the absence of environmental gradients.

Thus, in both standard population dynamics and range-evolution models, a statistical distribution of geographic range sizes under uniform and constant environments will be transient and is clearly not adequate to form the basis for broad-scale aggregate RSFD patterns that underlie the MDE hypothesis. This leaves the geometric constraints concept without a biologically meaningful theoretical foundation, at least as a general null model for variation in species richness. Instead, a population dynamics approach generates the null expectation of no diversity gradient in the absence of environmental driving factors to generate an RSFD. We suggest that this is a more relevant approach for understanding how groups of individuals distribute themselves in space that more accurately represents the underlying biological nature of ranges.

Conclusion

We have focused our critique of the MDE by arguing that the RSFD could not arise under uniform environments, so the MDE cannot be considered a null model against which environmental factors can be contrasted. And even if MDE-like patterns can appear under some combinations of parameters in some models, we doubt that MDE can be treated as a general null model for broadscale patterns in species richness.

We see two possible outcomes of the current debate around the MDE issue. If one accepts the criticism we present here, it follows that empirical tests of MDE models cannot advance our understanding of why diversity gradients exist, and we reiterate the previous recommendation of Hawkins and Diniz-Filho (2002) that the MDE should be dropped as a potential explanation for diversity gradients. We believe it is self-evident that if we cannot identify precisely why the observed RSFD arises, fitting an MDE model teaches us nothing of the underlying processes that produce patterns of species richness. On the other hand, if the fundamental conceptual problem we point out here is not accepted (a serious error, in our opinion), empirical tests should be conducted under the best possible conditions, avoiding the numerous problems discussed in detail by Colwell et al. (2004) and Pimm and Brown (2004). Only by considering simultaneously both the conceptual

basis and empirical results of the MDE will it be possible to advance in the debate on the ecological and historical processes driving species richness.

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