



The mid-domain effect: it's not just about space

Ecologists and biogeographers have long sought to understand how and why diversity varies across space. Up until the late 20th century, the dominant role of environmental gradients and historical processes in driving geographical species richness patterns went largely undisputed. However, almost 20 years ago, Colwell & Hurr (1994) proposed a radical reappraisal of ecological gradient theory that called into question decades of empirical and theoretical research. That controversial idea was later termed the 'the mid-domain effect': the simple proposition that in the absence of environmental gradients, the random placement of species ranges within a bounded domain will give rise to greatest range overlap, and thus richness, at the centre of the domain (Colwell & Lees, 2000) (Fig. 1a). The implication of this line of reasoning is that the conventional null model of equal species richness regardless of latitude, elevation or depth should be replaced by one where richness peaks at some mid-point in geographical space.

In spite of the rapid accumulation of numerous empirical datasets conforming to the mid-domain null model across a wide range of taxa (Colwell *et al.*, 2004), opposition to the mid-domain hypothesis was staunch (e.g. Hawkins *et al.*, 2005; Zapata *et al.*, 2005). Opponents cited the porosity of geographical domains and the purported 'smuggling in' of environmental factors into the range size frequency distribution used to generate mid-domain null models as logical flaws (Hawkins *et al.*, 2005). The mid-domain debate reached its own peak in 2004–2005 with a series of reviews (e.g. Colwell *et al.*, 2004), comments (Hawkins *et al.*, 2005; Zapata *et al.*, 2005) and replies (Colwell *et al.*, 2005) in the *American Naturalist*. Despite little resolution, the debate around the mid-domain effect subsequently waned. However, the number of recent research papers (26 from 2011–2012 according to Web of Science) citing the mid-domain effect stands testa-

ment to its continued influence on ecological discourse.

Our intention here is to draw attention to a neglected, yet important manifestation of the mid-domain effect, namely the application of mid-domain models (also referred to as geometric constraint models) to non-spatial domains. If individual species have ranges that exist not just in geographical space but also in environmental factors, such as temperature, rainfall, pH, productivity or disturbance, shouldn't we also expect mid-domain richness peaks along non-spatial gradients? A mid-domain model applied to non-spatial gradients predicts the maximum potential richness for every value of an environmental factor. As with spatial mid-domain models, realized richness would probably be less, but the limits to richness are still predicted to be hump-shaped. Indeed, hump-shaped relationships emerge with remarkably high frequency across various non-spatial gradients. For instance, two of ecology's most fundamental, albeit controversial theories – the productivity–diversity relationship and the intermediate disturbance hypothesis – predict mid-domain peaks in species richness. However, the potential of non-spatial mid-domain models has gone largely ignored.

The notion that mid-domain models may have non-spatial applications has been noted before (e.g. Colwell & Lees, 2000). However, only six studies have actually employed mid-domain models to inspect richness responses along non-spatial gradients, including sea temperature (Brayard *et al.*, 2005; Beaugrand *et al.*, 2013), estuarine temperature and salinity (Carranza *et al.*, 2008), light (Lusk *et al.*, 2006) and time (Morales *et al.*, 2005; Tiwari *et al.*, 2005). All six studies found evidence for a non-spatial mid-domain effect. Given the paradigm-shifting ramifications of a mid-domain null expectation along any non-spatial gradient, we venture there is an imperative for further quantitative inquiry.

The dearth of studies that have investigated non-spatial mid-domain effects points to either a lack of awareness of their potential relevance or an uncertainty in their implementation. Having addressed the former above, below we briefly consider the latter, beginning with an illustrated example. Consider a temperature gradient, from the coldest surface temperatures on Earth to the hottest temperatures. The maximum and minimum temperatures define the boundaries of the domain. Species occupy portions of this domain (for instance, emperor penguins occupy a small range towards the cold end of the scale). To apply mid-domain models to temperature gradients, species' observed temperature ranges are randomly assigned to the domain. As with the spatial ranges, assuming species' temperature ranges are of intermediate size with respect to the temperature domain, mid-domain models will predict the greatest number of overlapping ranges in the middle of the domain; that is, they predict the greatest species richness at intermediate temperatures (Fig. 1b). Examining the latitudinal gradient in species richness solely from the perspective of a mid-domain effect along a temperature gradient, we thus predict species richness to peak somewhere around mid-latitudes, i.e. a bimodal pattern (Fig. 1c). Although a mid-latitude richness peak is at odds with the wealth of empirical data evidencing a monotonic increase in richness towards the equator, in some environments the predicted bimodal gradient actually occurs with extraordinary frequency (Rutherford *et al.*, 1999). Indeed, Brayard *et al.* (2005) demonstrated that an observed bimodal latitudinal richness gradient in marine plankton can arise from the combination of a geographical and a thermal mid-domain effect. As such, under warming temperatures, combined spatial and non-spatial mid-domain models may be expected to predict a poleward shift in transequatorial richness peaks for some taxa.

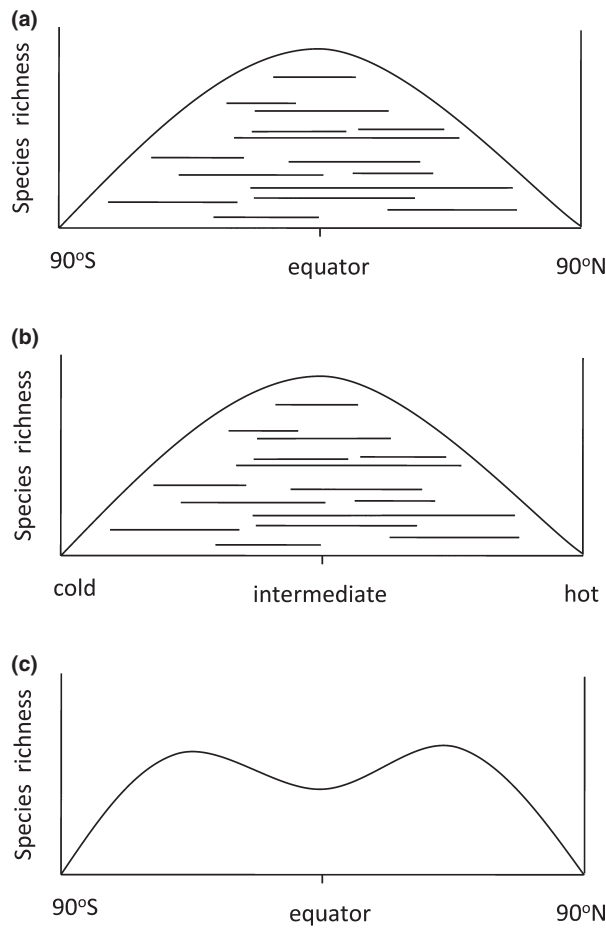


Figure 1 (a) The traditional mid-domain model (Colwell & Hurtt, 1994); (b) the same mid-domain model applied to a temperature-based domain; (c) the predictions from (b), mapped back on to geographical space. The curve in panel (c) is an example only. Its real shape would depend on the specifics of the temperature domain considered [most importantly, the slope of the temperature gradient (Brayard *et al.*, 2005), whether you define the domain according to lethal temperatures or mean temperatures, and what temporal scale you consider temperature data over]. The most appropriate options would depend on the biology of the taxa being considered.

Although we used temperature as an example, in reality, species distributions are almost always determined by a range of factors acting in concert. Thus, we need a way to combine information from models based on different factors. A simplified approach would be first to map the predictions from the temperature domain onto latitudinal space by taking the predicted number of species for each temperature, and mapping them on to the locations in the spatial domain which experience that temperature. The same process can be applied to predictions based on net primary productivity, rainfall, or any other variable for which the spatial distribution is known. Once the predictions are in a common currency (e.g. the number of species expected at a given

location), we can use standard statistical techniques (e.g. generalized linear models) to investigate the proportion of variation in the observed data explained by models based on the different variables, and by their interactions. Predictions from a purely spatial mid-domain model could be included as one of the variables of interest. Examining residual variation from predictions generated by these multiple-factor mid-domain models should lend insight into the underlying causes of diversity gradients in a more powerful way than was possible with a single variable alone. There is, of course, considerable scope for future work exploring different methodological approaches to non-spatial mid-domain models on both real and simulated datasets.

Several of the challenges encountered in applying spatial mid-domain models will also apply to non-spatial mid-domain models, for example what is the most appropriate approach to compiling the range size frequency distribution, how should the domain limits be defined, and what is the appropriate taxonomic resolution? In addition, given the existence of robust ecological theory invoking trade-offs that generate just the same kind of unimodal patterns anticipated by non-spatial mid-domain models, distinguishing stochastic phenomena from genuine ecological responses will necessitate careful statistical analyses. Nevertheless, we suggest that the potential ramifications of non-spatial mid-domain models are of sufficient magnitude to warrant much greater attention.

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