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TECHNICAL COMMENT

Testing, as opposed to supporting, the Mid-domain Hypothesis: a response to Lees and Colwell (2007)

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Abstract

Both our analysis (Kerr *et al.* 2006), and Lees and Colwell's (2007) reanalysis, of patterns of bird and mammal diversity on Madagascar show that the central peak of richness predicted by the Mid-Domain Hypothesis (MDH) is not observed. Lees and Colwell emphasize an observation consistent with MDH predictions: a latitudinal mid-domain richness peak in the rainforest biome. They find (but do not mention) that no analogous peak is observed in the other two main Madagascan biomes. MDH fails nearly all its tests in Madagascar.

Keywords

Species richness, mid-domain effect, MDE, range, diversity, Madagascar, birds, mammals, biogeography.

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The Mid-domain Hypothesis proposes that, 'a mid-domain peak or plateau in species richness (hereafter MDE) is inevitable for virtually any set of ranges, theoretical or empirical, when these ranges are randomly placed within a bounded geographical domain, in the complete absence of any supposition of environmental gradients within the domain' (Colwell & Lees, 2000).

Kerr *et al.* (2006) tested for MDEs in the endemic birds and mammals of Madagascar. Madagascar is a clearly bounded domain with many endemic species. Environmental (e.g. climatic) gradients on Madagascar are not strongly collinear with MDE model predictions, so the two hypotheses can be unambiguously evaluated in combination, as advocated by Colwell & Lees, 2000.

Richness among birds and mammals shows no mid-domain peak with respect to latitude after controlling for variation in area among latitudinal bands. In two-dimensional analyses using equal-area quadrats, richness again has no mid-domain peak for either birds or mammals.

Lees & Colwell (2007); hereafter L&C) contest our conclusions. They re-analysed our original spreadsheets and found a summation error for bird richness in latitudinal bands. To this, we plead guilty. However, L&C fail to mention that correcting the error does not change our original observation: after controlling for area, bird richness shows no mid-domain peak. Neither is there a mid-domain peak for mammals. The Mid-domain Hypothesis failed all four tests we constructed, and L&C present no evidence to the contrary.

Remarkably, L&C suggest that Madagascar is an inappropriate domain in which to test MDEs 'because environmental drivers are expected to overwhelm the stochastic effects of geometric constraints'. Yet, mid-domain theory (Colwell & Lees, 2002) proposes that MDEs occur in *all* bounded domains, irrespective of environmental gradients. L&C state that MDEs are 'one among many contributing factors that combine and interact to determine spatial patterns of species richness'. Accordingly, we tested for MDEs in combination with environmental variables and could not detect them. Oddly, Romdal *et al.* (2005) find the entire New World to be an acceptable domain in which to look for MDEs. This domain obviously includes dozens of biomes and massive environmental gradients. Objecting to Madagascar because of its environmental gradients appears to be *post hoc* protection of their hypothesis against test. Indeed, it contradicts the basic premise of mid-domain theory that MDEs necessarily occur in *any* bounded domain.

L&C argue that MDEs are clearer within biomes. To show this, they divided Madagascar into three transects, corresponding roughly to three biomes. L&C then note that richness shows a mid-latitudinal peak on the eastern transect. L&C did not test the stronger prediction that the shape of the observed peak corresponds to the predicted shape, as proposed by Colwell *et al.* (2004) and Romdal *et al.* (2005). L&C show, but fail to point out, the absence of any richness peak for the other two transects. Thus, the Mid-domain Hypothesis passed its weakest test in two cases

(birds and mammals, three transects each) and fails in four. L&C show that MDEs are *not* generally most apparent within biomes.

L&C present other objections about whether or not richness shows mid-domain valleys, or decreases with latitude, or differs among biomes. That is all irrelevant, because none of it addresses predictions of the Mid-domain Hypothesis.

Kerr *et al.* (2006) suggested that Lees *et al.* (1999) observed MDEs in the Madagascan rainforest because they inferred 89.4% of species presences by interpolation between observed presences. Interpolation across the mid-domain necessarily increases richness in the middle. Lees *et al.* argued that interpolation was unimportant in their study; in contrast to that assertion, we find that observed patterns of richness in their data are equally consistent with either interpolation artefacts or MDE Currie & Kerr (in press).

L&C find it ironic that Kerr *et al.* (2006) used range maps, which also involve interpolation, to test MDEs in Madagascar. Interpolated ranges potentially inflate apparent MDEs, yet the Madagascan MDE is still missing. L&C's allegation of 'range spillover' applies to any rasterized data (i.e. presences in grid cells or in transects) whether the data come from range maps or their own point presences. A single observed presence, or a range edge that enters a grid cell, is recorded as a presence in the entire cell.

To summarize, L&C's objections are lawyerly, rather than judicious. The critical issue is whether MDE-predicted peaks of richness are observed. For the island as a whole, they are not. Within biomes, they are not observed in four tests out of six. In the other two cases, L&C did not follow their own recommendation (Romdal *et al.* 2005) to test whether the shape of the observed peak is consistent with the MDE-predicted shape. In sum, the Madagascan data are consistent only with the weakest predictions of the hypothesis, and even then, infrequently. Furthermore, the positive results could equally reflect nothing more than interpolation across the mid-domain. L&C effectively argue that one must choose a domain very carefully to find evidence of mid-domain effects. With that, we can agree.

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