TECHNICAL COMMENT

# A strong Madagascan rainforest MDE and no equatorward increase in species richness: re-analysis of 'The missing Madagascan mid-domain effect', by Kerr J.T., Perring M. & Currie D.J. (*Ecology Letters* 9:149–159, 2006)

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## Abstract
By reanalysing inaccurately presented data of Kerr *et al.* (2006), we refute their claims that area-corrected species richness of endemic Madagascan birds and mammals increases toward the Equator and is best explained by environmental factors, and that the rainforest mid-domain effect (MDE) Lees *et al.* (1999) demonstrated is artefactual.

## Keywords
Biogeography, birds, latitudinal gradient, Madagascar, mammals, MDE, mid-domain effect, range size, species richness.

*Ecology Letters* (2007) 10: E4–E8

Given the prominence accorded to the Lees *et al.* (1999) study of Madagascan biogeography (henceforth LKA) (e.g. Colwell & Lees 2000; Pimm & Brown 2006), any new study of MDE and other potential drivers of species richness patterns in Madagascar must meet LKA on its own terms. Unfortunately, Kerr *et al.* (2006) (henceforth KPC) fail to engage the principal findings of LKA, instead constructing obliquely related models and analyses. Here, we reanalyse the data of KPC (which we thank them for providing), and reconcile their findings with those of LKA (which we here reaffirm) by correcting substantial quantitative and analytical errors and misinterpretations.

We address five principal claims made by KPC: (1) that the entire island of Madagascar is the 'classic case in which MDE's should occur'; (2) that the mid-island peak in richness that they document accurately for mammal latitudinal band sums but underestimate for birds (KPC Fig. 4a) is caused by an area effect (the island is wider at mid-latitudes) rather than by MDE; (3) that their analysis reveals 'a latitudinal gradient of increasing richness towards the equator' for birds and mammals; (4) that 'in contrast to the relationship with MDE predictions, species richness is strongly related to environmental factors' for these groups; and (5) that the rainforest MDE documented by LKA 'seems likely to have reflected methodological artefacts'.

(1) MDE is one among many contributing factors that combine and interact to determine spatial patterns of species richness (Willig *et al.* 2003; Colwell *et al.* 2004, 2005). Because strong environmental drivers are expected to overwhelm the stochastic effects of geometric constraints (Rangel & Diniz-Filho 2005), MDE is more likely to affect patterns of richness within biomes than across contrasting biomes (Colwell *et al.* 2004). Considering the island as a whole, with its pronounced environmental gradients and massive interior anthropogenic wasteland, Madagascar is actually an unlikely place to expect any substantial island-wide effect of MDE. KPC's whole-island maps (KPC Fig. 2a,c) confirm for endemic mammals and birds the key finding of Lees *et al.* (LKA Fig. 8a,b, p. 556) that there is no apparent whole-island MDE for a much broader set of groups.

(2) KPC dismiss a mid-island latitudinal richness peak (KPC Fig. 4a) after showing that whole-island latitudinal band sums 'adjusted' for band area (by taking residuals from a regression of log $S$ on log $A$) show no such peak (KPC Fig. 4b,c). Our re-analysis of KPC's data (Fig. 1), which avoids any confounding effect of longitudinal area by using latitudinal transects of constant width, shows that the north–south MDE in

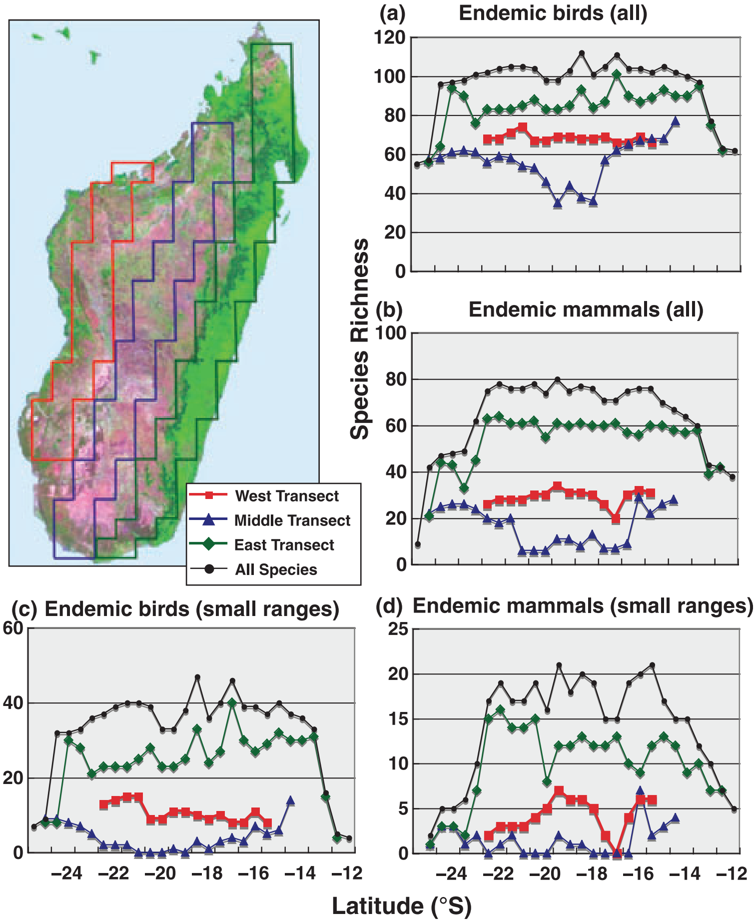


**Figure 1** Latitudinal patterns of species richness of birds and mammals endemic to Madagascar, based entirely on the data set of Kerr *et al.* (2006) = (KPC). Three north–south transects are shown superimposed on the Mayaux *et al.* (2000) map. The East Transect follows the rainforest biome (including secondary forest) studied by Lees *et al.* (1999) (LKA), the Middle Transect runs through the dry centre of the island (almost entirely alien grasslands), while the West Transect includes dry coastal forest and anthropic grassland. Each transect is 1° of longitude wide (two half-degree quadrats) at all latitudes with limited overlap of coastlines, based on a 0.5° of latitude equal area polygon lattice fitted to KPC Fig. 2a. The graphs plot species richness for each latitudinal half-degree, based on a re-analysis of KPC's digitized distributional data. In the graphs, for all endemic birds and all endemic mammals, the black lines (filled circles) plot the total richness for full latitudinal bands, as in KPC (their Fig. 4a, corrected here for birds; see below), whereas the green line (diamonds) shows richness along the East Transect, the red line (squares) along the Middle Transect, and the blue line (triangles) plots richness along the West Transect. KPC claim that the longitudinal shape of the island explains the mid-latitudinal peak in richness, presumably on the assumption that differences in band sum richness are caused by latitudinal variation in sampling window area (Harte & Kinzig 1997). Our transect data (which by definition lack any planar longitudinal area sampling effect) reveal, instead, that the peak is largely driven by the rainforest mid-domain effect (MDE) in the East Transect, as documented by LKA. Within the East Transect, smaller range sizes (those ranking below median range size, most of which are nonetheless substantial) drive the MDE, as shown in the graphs for small ranges. [Similar plots for ranges larger than the median are flat-topped, as expected for ranges approaching domain size, e.g. run RangeModel 5 (Colwell 2006) with a range-size minimum of > 0.7]. KPC's claim that area-corrected richness increases equatorward (towards the right side of graphs) is not supported by the transect data, which are virtually free of planar sampling window effects. The dip in richness in the centre of the Middle Transect is clearly a result of total removal of endemic species habitat towards the centre of Madagascar, while the northern end borders the richer, rainforest biome. In the KPC analysis, based on species–area (SAR) residuals, the high richness of the rainforest biome is misleadingly discounted by the KPC area adjustment at mid-latitude, whereas the rainforest of the narrowing, northern part of the island contributes to band sums with increasingly full strength, producing an illusory northward increase in richness. Our reanalysis uncovered substantial errors in the KPC results for birds: (1) the number of rainforest-endemic birds is about 40 (Langrand 1990, p. 21), not 16 as they report, thus mistakenly judging the number too low for a biome-level analysis; (2) errors in the band sums shown for birds in KPC's Fig. 4a vary from 2% to 79% and are especially off at mid-latitudes, hiding a clear mid-latitude richness plateau (Fig. 1a).

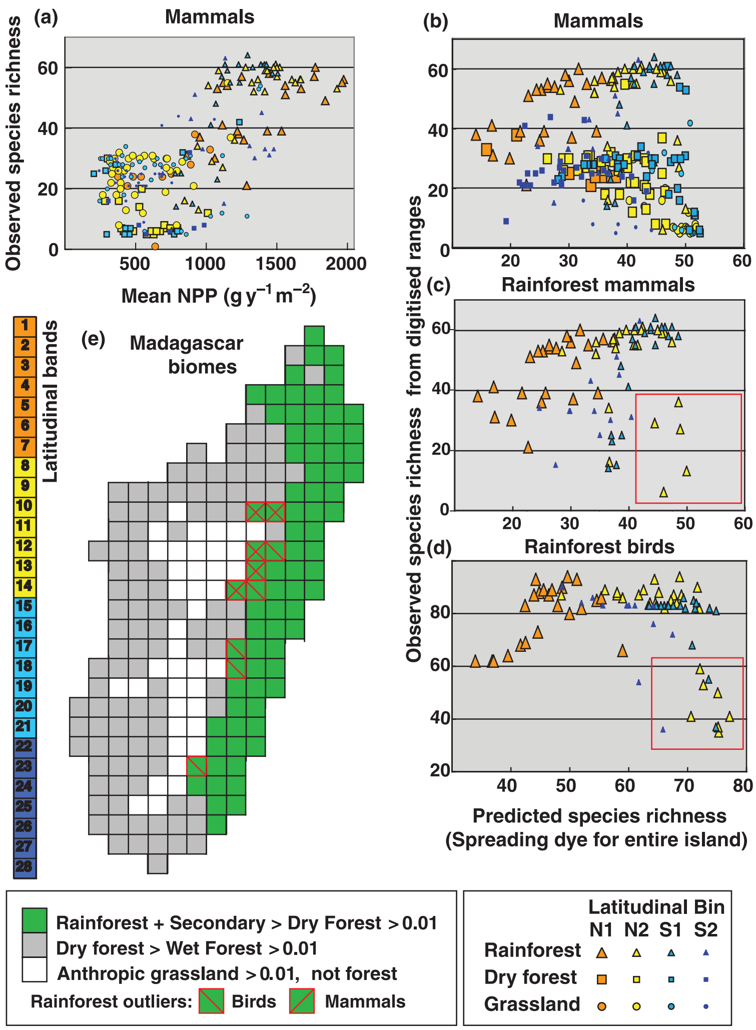


**Figure 2** Observed species richness of Madagascar endemic birds and mammals in relation to mean net primary productivity (NPP) and whole-island (2-D) mid-domain effect (MDE) predicted richness. (a) Endemic mammal species richness plotted against NPP [$n = 228$; reanalysis of Fig. 6 Kerr et al. 2006 (KPC)]. The points are coded by biome (symbol shape) and four latitudinal bins (north to south: N1, latitudinal bands 1–7; N2, bands 8–14; S1, bands 15–21; S2, bands 22–28) displayed as increasing symbol size and colour warmth towards the Equator (coloured latitudinal bands on left of map). Notice that species richness peaks within mid-latitudes of the rainforest biome (triangles of intermediate symbol sizes and colours), revealing the rainforest MDE documented by Lees *et al.* (1999). The overall correlation between species richness and NPP apparent in the graph is driven almost entirely by spatially autocorrelated longitudinal contrasts in NPP and richness between rainforest (triangles) and less productive habitats (dry forest, squares and anthropic grassland, circles). The graph shows no evidence of an equatorward increase in productivity or species richness (symbol sizes and colors are mixed throughout). (b) Scatterplot of observed endemic mammal species richness vs. richness predicted by the 'entire island spreading dye' model of KPC, which they based on digitized range data from Garbutt's (1999) field guide. KPC's corresponding plot for Madagascar endemic birds (KPC, Fig. 5) for all map cells is very similar. (c) Observed and MDE-predicted endemic mammal species richness for the rainforest map cells in (b). (d) Observed and MDE-predicted endemic bird species richness for the rainforest map cells in KPC's Fig. 5. (e) Madagascar biomes at a dominance threshold of 1% remaining forest, based on area sums of classified forest fragments in the Mayaux *et al.* (2000) map intersected with the KPC lattice (using ESRI's GIS ArcView 3.2). Despite the highly inappropriate treatment of the entire, climatically heterogeneous island as a single domain, and contrary to the caption in KPC's Fig. 5, there is nevertheless a positive correlation between observed and predicted richness for both datasets within the rainforest biome (c and d, triangles). This correlation appears clearly once western outliers are removed: e.g. the points in the red outlined squares in Fig. 2c,d, which correspond to the cells outlined in red squares in the map (Fig. 2e, see map caption for details); these are all marginal cells bordering the interior of Madagascar (where natural habitat has been > 99% eliminated: white areas), and thus have both low richness and are geographically closer to the (island centroid) origin of the spreading dye algorithm. Contrary to expectations of equatorward trends in species richness, but in accord with MDE, observed species richness is higher in mid-latitudinal bins (intermediate colours and point sizes), whereas richness is lower for the two extreme latitudinal bins.

rainforest biota documented by LKA, not the shape of the island, drives the KPC band sums. Moreover, we found substantial errors in the KPC results for birds, which spuriously introduced a mid-latitudinal valley of richness (KPC Fig. 4a; see our Fig. 1 caption).

(3) Our transect analysis (Fig. 1) refutes the supposed latitudinal increase in endemic species richness from south to north (KPC Fig. 4b,c) for 'area-adjusted' data: both birds and mammals show an overall N–S symmetry in total richness for all three constant–area band transects, revealing no sensitivity of *local* richness to island shape, while documenting a strong MDE in their data set.

(4) KPC's demonstration that 'environmental factors' (forest cover, KPC Table 1, and NPP, KPC Fig. 6) are correlated with richness at the whole-island scale is correct, but misleading. Figure 2a shows that KPC's richness-NPP correlation is driven mostly by the stark contrasts between the species rich, high-NPP rainforest biome *versus* the barren interior and dry forests, including the southwest subarid zone. KPC Fig. 6 is in fact consistent with both within-biome MDE (as demonstrated for rainforest by LKA and confirmed for KPC's data in our Fig. 1 East Transect and Fig. 2a) and between-biome productivity differences. It fails to support KPC's claim of a latitudinal richness gradient 'just as climate-based hypotheses predict'.

(5) KPC's claim of 'methodological artefacts' in LKA is wholly unjustified, as the two issues mentioned were dealt with exhaustively (interpolation on LKA pp. 535–537 and LKA Figs 2 and 8; sampling effort on LKA p. 539 and LKA Fig. 9). Although interpolation augments apparent MDE patterns (Grytnes & Vetaas 2002), it is also a legitimate means of estimating true ranges from sparse sampling data, especially for mobile organisms. In contrast to LKA's empirical point data, georeferenced meticulously from museum specimens or records and interpolated using explicit criteria, it is therefore ironic that KPC's own data is based entirely on rangefills from fieldguides [e.g. 22% of Langrand's (1990) maps are completely uninformative regarding biogeographic pattern in the island interior]. Instead of attempting to replicate LKA, KPC compound error by digitizing already over-interpolated ranges, and increase spillover at range margins by using a coarser spatial scale.

In summary, with its lower resolution data, computational errors (bird data), misleading analysis, and unsupported inferences, the KPC study fails to undermine the conclusions of LKA, and misrepresents its scope. Nevertheless, we endorse the development of predictive, multi-biome models of species richness that integrate environmental with stochastic causes, for Madagascar (as initiated by KPC) and elsewhere (e.g. Storch *et al.* 2006; Rahbek *et al.* 2007).

## ACKNOWLEDGEMENTS

We are grateful to Jeremy Kerr and his coauthors for providing us with the digitized range data and environmental information used by KPC. Colwell was supported by the US National Science Foundation (DEB-0639979). ESRI is acknowledged for donating Arcview GIS software to Lees.

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Editor, Marti Anderson
Manuscript received 2 March 2007
First decision made 8 March 2007
Manuscript accepted 16 March 2007