

## LETTER

## The missing Madagascar mid-domain effect

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**Abstract**

Species richness varies enormously across geographical gradients, a well-known phenomenon for which there are many hypothesized explanations. One recent hypothesis uses null models to demonstrate that random re-distribution of species' ranges within a given domain leads to a 'mid-domain effect' (MDE): increasing species richness towards the centre of the area. Madagascar is especially well-suited for empirical evaluation of mid-domain models by virtue of its large endemic fauna and its clearly defined boundaries. Lees *et al.* [*Biol. J. Linn. Soc.* **67** (1999) 529] observed patterns of species richness consistent with MDEs in the Madagascar rainforest (a slim, north–south belt). In this study, we test one-dimensional and two-dimensional mid-domain model predictions for the birds and mammals of the entire island of Madagascar. When only latitudinal extents of species' distribution are considered, patterns of richness in Madagascar show an MDE. However, this pattern disappears for both taxa after accounting for the tendency of latitudinal bands nearer the middle of the country to be larger. Two-dimensional mid-domain model predictions of species richness are qualitatively opposite to observed patterns. Instead, island-wide spatial gradients of species richness in Madagascar relate strongly to patterns of primary productivity and amount of remaining natural habitat. Earlier work that showed a mid-domain peak within the rainforest biome (effectively after controlling for climate and natural habitat) seems likely to have reflected methodological artefacts. The classic case in which MDEs should occur is, in fact, inconsistent with the mid-domain hypothesis.

**Keywords**

Geographical ecology, mid-domain effect, null models, remote sensing.

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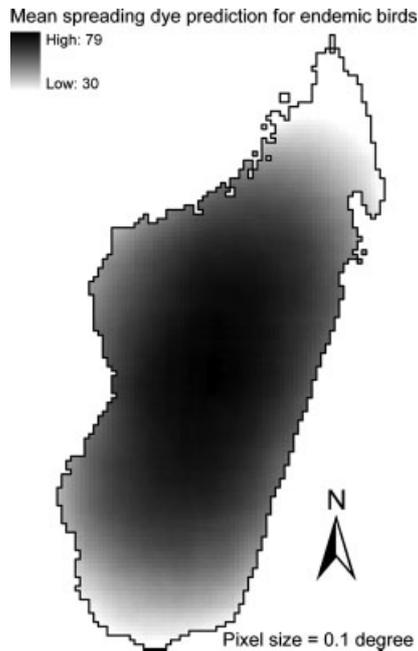
**INTRODUCTION**

Although broad-scale geographical variability in species richness is one of the most widely observed and studied biotic patterns, the processes that give rise to it remain controversial. Additional entries in the long list of potential explanations (see Currie 1991; Rohde 1992; Palmer 1994; Rahbek & Graves 2001) for species richness gradients continue to accumulate at a brisk pace (e.g. Dynesius & Jansson 2000); however, those with the greatest empirical support postulate that richness gradients reflect gradients in characteristics of the contemporary environment such as climate (e.g. Wright *et al.* 1993; Kerr *et al.* 1998; Hawkins *et al.* 2003; Currie *et al.* 2004) or habitat heterogeneity (e.g. Kerr & Packer 1997; Kerr *et al.* 2001).

Recent work hypothesizes that geographical patterns of species richness could result, in part, from constraints on

the placement of species distributions within defined areas, apart from any underlying biological response to environmental gradients within the bounded space (Colwell & Hurtt 1994; Lees *et al.* 1999; Jetz & Rahbek 2001). Consider a geographical area with 'hard' boundaries (which have biological meaning, e.g. coastlines for terrestrial, non-volant species) beyond which species' ranges cannot extend. If species' ranges are randomly placed within those boundaries, then a mid-domain effect (MDE) of increasing species richness towards the centre of the space should appear (Fig. 1).

This intuitive mid-domain concept has been operationalized in many different mid-domain models. The simplest MDE models are one-dimensional (1D), examining predicted richness along a single (usually N–S) axis (e.g. Colwell *et al.* 2004, their Table 1). Approaches to 1D models have been thoroughly discussed elsewhere (cf. Colwell 2000;



**Figure 1** Predicted patterns of endemic bird species richness in Madagascar from this study's two-dimensional, spreading dye null model. Predicted species richness increases (lighter shades) towards the centre of a geographical space and is lowest towards 'hard' boundaries of the space (coastlines, in the case of Madagascar). Predictions for endemic mammals are qualitatively identical.

Zapata *et al.* 2003; Colwell *et al.* 2004). A variety of models have also been proposed to describe the variation of richness in two dimensions (Lees *et al.* 1999; Bokma & Monkkonen 2000; Bokma *et al.* 2001; Diniz-Filho *et al.* 2002). Most recently, spreading dye models (described and implemented below) have been used to conserve the range size frequency distributions of study organisms when building two-dimensional (2D) MDE surfaces from randomly generated individual ranges (Jetz & Rahbek 2001, 2002). All MDE models predict that endemic species richness decreases away from the geographical midpoint of the study region.

The purpose of this study is to test (as advocated by Colwell *et al.* 2004) whether patterns of endemic species richness of Madagascan birds and mammals are consistent with MDE predictions. Madagascar is the archetypal situation where one would expect to observe MDEs: a space with hard boundaries (ocean) with a large number of endemic species. Lees *et al.* (1999) reported that endemic species richness in several taxa in Madagascar (including birds, tenrecs, lemurs and rodents) is highest around the central latitudes of the Madagascan rainforest belt, as predicted by simple, 1D MDE models. Pimm & Brown (2004) present this example as an 'impressive victory' for the mid-domain hypothesis because the mid-domain hypothesis

predicted maximum richness in the middle of Madagascar, in contrast to the prediction of competing hypotheses that richness should be highest at the end of the island nearest the equator.

To test mid-domain predictions, we constructed a spreading dye mid-domain model (qualitatively similar to that of Jetz & Rahbek 2001, 2002). Using this model, we generate MDE predictions in one and two dimensions for both endemic Madagascan birds and mammals. Because this method conserves range size frequency distributions, MDE-predicted gradients of species richness gradients depend, to some extent, upon how broadly distributed the species are. The spreading dye model predicts that bird and mammal richness both peak at the midpoint of the geographical space; however, richness declines the most towards the northern and southern coasts.

We also test the competing hypothesis that patterns of richness are related to characteristics of the contemporary environment. Specifically, we test whether patterns of richness are related to climate (temperature and precipitation; cf. Hawkins *et al.* 2003), vegetation cover measured using independently developed satellite land cover data (Defries *et al.* 1998; Mayaux *et al.* 2000; Kerr *et al.* 2001) and topographic variability (Kerr & Packer 1997). We further tested whether observed distributions of species in Madagascar are related to the amount of remaining forested habitat. Significant extents of forested habitat remain in some regions, particularly near the eastern coastlines, the Masoala Peninsula in the Northeast, and in the South. However, the introduction of several non-native vertebrates (e.g. the black rat, *Rattus rattus*) that have since spread throughout much of the island, as well as other forms of human disturbance such as illegal logging, suggest that nowhere on the island is free of significant anthropogenic impacts.

The most important way in which the present study and the earlier work of Lees *et al.* (1999) differ are the study domains. Lees *et al.* generated maps of species richness for all of Madagascar; however, they restricted their analyses to the Madagascan rainforest biome. They did this, '[s]o as to provide a more focused analysis using a null model' (p. 537) and because, 'the potential linearity of species ranges in Madagascan rainforest, and the fact that it does not straddle the equator, provides an excellent opportunity to test environmental and null gradient models for explaining latitudinal patterns of richness within a single biome' (p. 531). In contrast to Lees *et al.* (1999), we did not limit our study to rainforest areas because few of the endemic mammal and bird distributions in Madagascar are limited to a single biome. For example, of the 200 land bird species in Madagascar, Langrand (1990) lists 16 whose distributions are limited to rainforest, and six others that occur principally in rainforest. The remaining species' distributions span

**Table 1** Conditional autoregressive regression models relating species richness patterns to contemporary environmental factors in Madagascar. MDE predictions of species richness were included in the models, but they were either non-significant or were significantly negatively correlated with observed richness. All variables are significant at  $P < 10^{-4}$  ( $n = 228$ ). Log-likelihood values for null statistical models (i.e. endemic species richness = 1) are -1235 (birds) and -1264 (mammals), respectively. 'VGT' refers to land cover data derived from the SPOT4/Vegetation satellite sensor and 'AVHRR' refers to data collected from NOAA14/Advanced Very High Resolution Radiometer satellite sensor (see Kerr & Ostrovsky 2003). Magnitudes of  $t$ -values indicate variable importance

Dependent variable	Independent variable	Coefficient	$t$ -value	Log-likelihood	$R^2$
Endemic bird richness	Forest extent (VGT)	0.34	7.3	-1091	0.72
	Mean NPP (AVHRR)	0.061	5.7		
	Mean NPP (AVHRR) <sup>0.5</sup>	-2.7	-4.5		
	Minimum elevation	-0.031	-12		
	Spreading dye prediction*	0.081	1.1		
Endemic mammal richness	Extent of human-modified lands (VGT)	-12	-4.8	-1164	0.58
	Mean NPP (AVHRR)	0.10	7.4		
	Mean NPP (AVHRR) <sup>0.5</sup>	-4.7	-5.8		
	Spreading dye prediction*	-0.052	-0.56		

\*Spreading dye predictions of endemic bird and mammal species richness were generated using observed range-size frequency distributions for these taxa. The marginal effect of the mid-domain prediction (i.e. after controlling for the other variables) is not significant for either endemic birds ( $P = 0.26$ ) or for endemic mammals ( $P = 0.58$ ). When the spreading dye predictions are used as the sole predictor of richness, this mid-domain prediction is significantly *negatively* related to observed patterns of endemic species richness for both taxa. In other words, observed patterns of richness are opposite to what would be expected if they derived from a mid-domain effect.

multiple biomes (Langrand 1990 Map 2 and species distribution maps). Thus, biome boundaries apparently do not constitute 'hard boundaries' upon which MDEs for these taxa are based. We discuss other differences between our approach and that of Lees *et al.* below.

## METHODS

### Species richness patterns

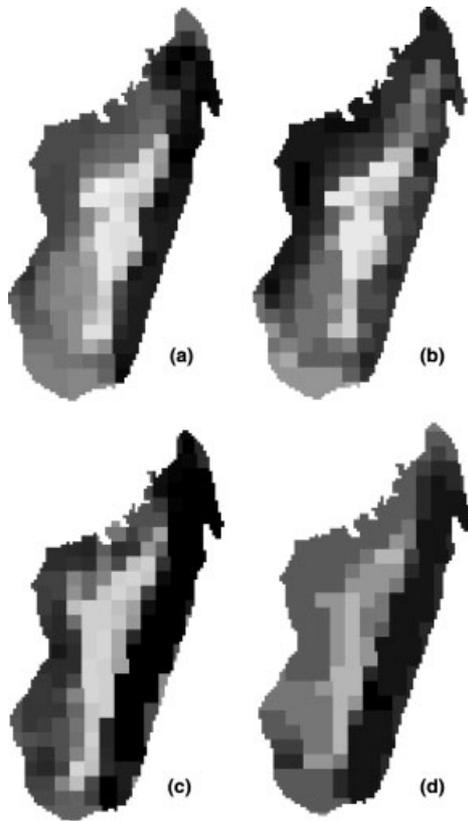
Species distribution data in the form of detailed distribution maps were collected for the birds and mammals of Madagascar. These taxa were selected because they appear to be the best-studied assemblages in Madagascar. Bird distributions were taken from Langrand (1990). Bird distribution maps were primarily based on extensive field observations made by Langrand and others during the 1980's. This information was complimented by older published observations, particularly on the distributions of rarer species. Mammal distributions were assembled from Garbutt (1999), a comparable resource that summarizes the distributions of each species based on surveys of field collections.

Distribution maps were digitized, georeferenced, and imported into a geographical information system. They were then superimposed to create maps of bird and mammal species richness (Fig. 2) as well as to collect range size data for all endemic species (Fig. 3). A grid of 0.5° latitude and variable longitude was created such that all fully terrestrial grid cells were of equal area. Predominantly marine quadrats were eliminated, resulting in a grid containing 228 cells.

Numbers of bird and mammal species were each tallied both for each latitudinal band (as the number of species that occurred anywhere within the entire band) and for each grid cell. Initially, richness was tallied separately for species with small ranges and those with large ranges. Small-ranged species were defined as having ranges  $\leq 20\%$  of the area of Madagascar ( $c. \leq 117,400 \text{ km}^2$ ). These were considered separately because MDE models predict that narrowly distributed species should exhibit little spatial variability in their richness patterns. Arc/Info Grid v. 8.2.3 (ESRI 2003), and PCI Geomatica 9.0 were used for all geographical analyses.

### Mid-domain predictions

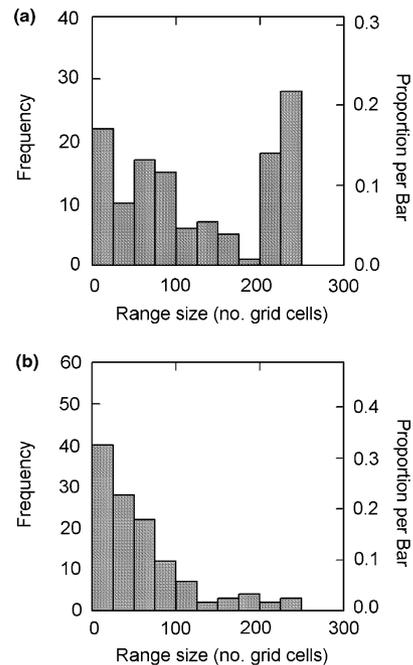
We derived both 1D and 2D mid-domain predictions by constructing a spreading dye algorithm. This algorithm randomly selects a pixel in the study domain (the land mass of Madagascar) to be the starting point for the modelled species' range. This pixel is then expanded by a small amount, as though it were a drop of ink fallen on the page. Then a pixel within the range is randomly chosen, and a second 'drop' falls on that pixel. If the drop passes the edge of range, the range is expanded accordingly. The algorithm repeats this process until the modelled range reaches the area of the range of a real endemic bird or mammal species in Madagascar. The modelled range is stored. The algorithm then repeats this process for all observed range sizes in a given taxonomic group, thus reproducing the taxon's range size frequency distribution. The stored ranges are then summed to create a spreading dye prediction of mid-domain



**Figure 2** Observed patterns of species richness in Madagascar for (a) endemic birds, (b) non-endemic birds, (c) endemic mammals, and (d) non-endemic mammals. All assemblages exhibit similar patterns of species richness. Except for the non-endemic birds, species richness tends to be highest (darker shades) in the eastern part of the country, where forest cover is greatest and primary productivity is highest. Non-endemic birds are most diverse nearest to Africa, which is presumably a source of colonists. Statistical analyses are presented only for endemic species, as non-endemics are not expected to show mid-domain effects.

species richness. We ran the algorithm, which was written in Arc/Info Macro Language for Arc/Info Grid GIS, 50 times for each taxon. We then calculated the mean MDE predictions of species richness for Madagascan endemic mammals and birds (Fig. 1).

We calculated predicted richness along a 1D, latitudinal gradient by tallying the number of simulated species' distributions that intersect each latitudinal band. Because the area of latitudinal bands in Madagascar increases substantially towards mid-latitudes, and because species richness is known to depend upon area, we calculated the area of latitudinal bands. We then tested for agreement between observed richness (log + 1 transformed) and 1D MDE predictions without log (area), vs. with log (area) in a multiple regression (see also Willig & Lyons 1998). Two-dimensional MDE predictions were generated by



**Figure 3** Range-size frequency distributions (RSFD) for endemic birds (a) and endemic mammals (b) of Madagascar. RSFDs are conserved in our spreading dye mid-domain effect models. These models make very similar predictions despite dissimilar underlying RSFDs.

tallying the number of modelled species ranges that overlapped each equal area grid cell covering the terrestrial mainland of Madagascar.

**Environmental characteristics**

For each grid cell, we determined the mean, minimum and maximum precipitation, temperature, and elevation. These were derived from 30 arc second data produced by the Shuttle Radar Topography Mission (SRTM), the Global Historical Climate Network, and other international organizations or projects (see Hijmans *et al.* 2004). Net primary productivity data were derived from global composites of Advanced Very High Resolution Radiometer (AVHRR) data at 1.1 km resolution (based on imagery collected from 1982 to 1989; Goetz *et al.* 1999) that had been atmospherically corrected and normalized for bidirectional reflectance distribution function effects. AVHRR data, when used for terrestrial earth observation, must be corrected for such effects (which account for atmospheric attenuation due to ozone, moisture, dust, etc., and the variability in the angle of the sun relative to the terrestrial surface and satellite across the >2000 km swath of the satellite's instantaneous field of view) or they cannot be accurately interpreted (see Cihlar *et al.* 1997; Kerr & Ostrovsky 2003).

Two recent land cover databases for Madagascar were also used to estimate habitat heterogeneity and the amount of remaining natural habitat present in each quadrat. The first of these was derived from the SPOT4/Vegetation (VGT) sensor (imagery from 1998 to 1999; Mayaux *et al.* 2000). The VGT sensor has a 1 km resolution (pixel size) and collects data in four spectral bands, including the three (red, near infrared and shortwave infrared) that are most effective for land cover (particularly vegetation) classification (De Boer 1993; Kerr & Ostrovsky 2003). The second land cover classification, also at 1 km resolution, is from AVHRR global pathfinder data (imagery from 1984; Defries *et al.* 1998). We measured land cover heterogeneity as the number of land cover classes occurring within each quadrat (Kerr *et al.* 2001; Kerr 2001). Most natural forest in Madagascar has been replaced with human-dominated landscapes that are classified as 'savannah' in satellite-based land cover classifications. The extent of non-savannah, non-urban land cover present in each grid cell was measured as an indication of the amount of remaining natural habitat.

Environmental conditions within large latitudinal bands crossing Madagascar vary enormously. We therefore did not attempt to aggregate and relate them to patterns of species richness in 1D (latitude only) analyses. For 1D tests, we restricted consideration of hypotheses to MDE predictions from spreading dye models and latitudinal band area.

### Statistical methodology

Spatial autocorrelation reduces the effective number of degrees of freedom for statistical analysis and can bias estimation of variable coefficients (Dale & Fortin 2002; Lichstein *et al.* 2002; Van Rensburg *et al.* 2002; Diniz-Filho *et al.* 2003; Tognelli & Kelt 2004). To test for spatial autocorrelation, we first examined the residuals from ordinary least-squares regression residuals (using the models presented in Table 1). Moran's  $I$  values were calculated with Rook's case (Sawada 1999) across a range of lag distances. We found that residuals from ordinary least-squares regression models were strongly autocorrelated, as observed in most analyses of geographical gradients of species richness (for detailed discussion of spatial autocorrelation, see Lichstein *et al.* 2002). For example, using the variables listed in Table 1, Moran's  $I = 0.70$ ,  $P < 0.05$ , for mammals at a lag of one quadrat, and it decreases to  $I = 0.15$ ,  $P > 0.05$  at a lag of four quadrats. Similarly, for birds,  $I = 0.53$ ,  $P = 0.002$  at a lag of one quadrat and decreases to non-significance at a lag of four quadrats. Consequently, instead of ordinary least squares, we used the conditional autoregressive models advocated in recent studies comparing ordinary least squares and spatial regression techniques for biogeography (Table 1; for statistical details, see Lichstein *et al.* 2002; Tognelli & Kelt 2004).

Bivariate plots of predictor variables (geometric and environmental) and bird and mammal species richness were examined to determine the shape of their relationships. Variables were entered interactively into conditional autoregressive models (see below) and retained or rejected based on their individual probabilities and each model's overall log-likelihood following the methodology of Lichstein *et al.* (2002). Coefficients of determination ( $R^2$ ) were calculated manually for each model (Nagelkerke 1991 in Lichstein *et al.* 2002). Statistically significant negative correlations between richness and mid-domain model predictions (i.e. patterns of species richness were opposite to, and therefore inconsistent with, mid-domain predictions) were excluded from lists of potential final models (cf. Anderson *et al.* 2000, 2001).

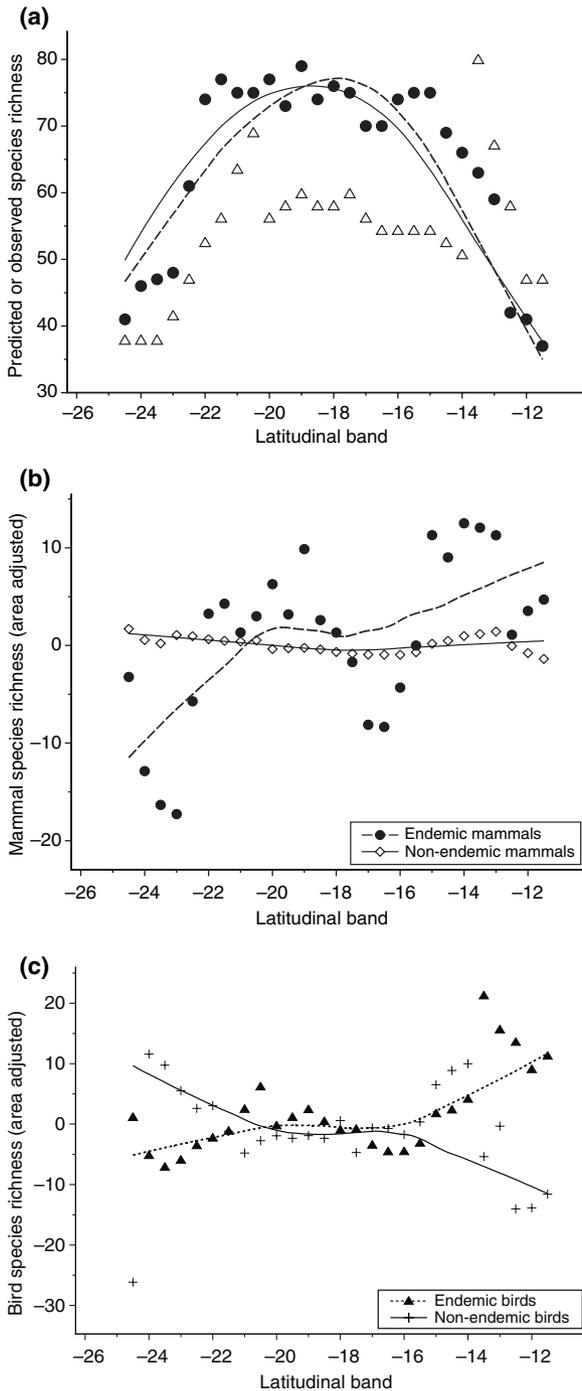
Arc/Info Grid v. 8.3 (ESRI 2003), and PCI Geomatica 9.0 were used for all geographical analyses and S-Plus 6.2 Spatial Statistics module (Insightful Corp. 2003) and Systat 10 (SPSS Inc. 2000) were used for statistical analyses.

## RESULTS

### Bird and mammal species richness patterns in Madagascar

Madagascan birds have broader ranges than mammals (mean range size for birds = 290 000 km<sup>2</sup>; mean range size for mammals = 146 000 km<sup>2</sup>; Wilcoxon rank sum test  $Z = 7.45$ ,  $P < 10^{-6}$ ). Consequently, endemic bird species richness (Fig. 2) exhibits less spatial variability across Madagascar than does endemic mammal species richness (coefficient of variation,  $CV_{\text{birds}} = 0.25$ ;  $CV_{\text{mammals}} = 0.60$ ;  $n = 228$  grid cells).

Previous studies of MDE models have noted that MDEs should be less pronounced among species with ranges that are small relative to the study area. About 55% of Madagascan mammals occupy <20% of Madagascar. The richness of these small-ranged species varies spatially in a very similar manner to the richness of broadly distributed species (Pearson  $r = 0.873$ ), in contrast to the MDE expectation. There are fewer narrowly distributed bird species (*c.* 25% of the 127 endemic bird species) so patterns of richness between narrowly and broadly distributed birds are poorly correlated. However, because species richness patterns among narrowly distributed birds and mammals are nearly identical to the patterns for all endemic Madagascan species (Pearson  $r > 0.985$ ), we report results for analyses of total endemic richness in this study. Species richness is highest in the east (Fig. 2a,c,d) except for non-endemic bird richness, which is highest in the west (nearest the African mainland, as might be expected; Fig. 2b). Endemic species richness for both birds and mammals is lowest in the centre of



**Figure 4** The simple, one-dimensional pattern (a) of endemic mammal (closed circles) and bird species richness (open triangles) in Madagascar appears to follow MDE predictions (solid line for mammals, dashed line for birds, both curves being generated using the spreading dye algorithm) unless band area is considered. Area-adjusted patterns of endemic mammal (b) and bird (c) species richness in latitudinal bands ( $n = 28$ ) are also presented. Latitudinal band area tends to increase towards the mid-latitudes of Madagascar. After statistically holding latitudinal band area constant, endemic bird species richness and endemic mammal species richness show a latitudinal gradient of increasing species richness towards the equator but no relationship with mid-domain model predictions. LOWESS curves (tension 0.7) illustrate the shape of area-adjusted relationships. Non-endemic species assemblages show little pattern after controlling for band area.

distributed bird species), the MDE predictions for these groups are very similar. Based on the average of 50 spreading dye model runs, the MDE-predicted bird and mammal richness per quadrat are very strongly correlated (Pearson  $r = 0.98$ ,  $n = 228$ ,  $P < 10^{-6}$ ; Fig. 4a). This correlation is stronger than the individual correlations typically observed between model runs for the same taxon (Pearson  $r$  range:  $c. 0.75-0.88$ ).

**One-dimensional mid-domain model consistency**

Endemic mammal species richness exhibits a pronounced mid-latitude peak that could be consistent with predictions of a simple 1D mid-domain model (Fig. 4a;  $R^2 = 0.70$ ,  $P < 10^{-4}$ ). The pattern is less clear for birds (Fig. 4a;  $R^2 = 0.15$ ,  $P = 0.041$ ). For both taxa, latitudinal band area is a better predictor of endemic species richness (birds:  $R^2 = 0.59$ ,  $P < 10^{-4}$ ; mammals:  $R^2 = 0.84$ ,  $P < 10^{-4}$ ). After controlling for the influence of latitudinal band area, mammal richness is not significantly related to MDE-predicted richness (Fig. 4b). For birds, mid-domain predictions of richness remain significant after controlling for area, but correlate negatively with richness, which is entirely inconsistent with mid-domain predictions. For both endemic bird and mammal assemblages, 1D, area-controlled richness shows the typical pattern of increasing species richness towards the equator.

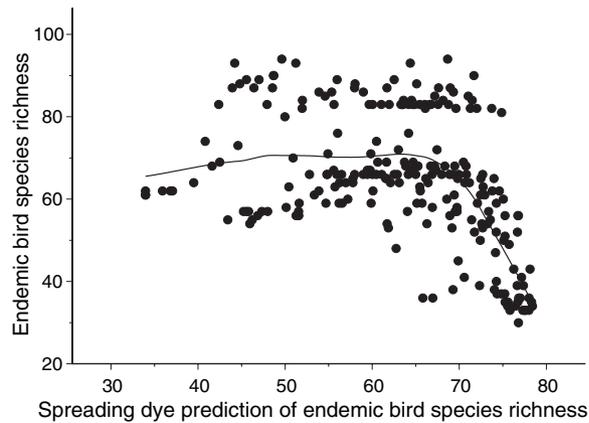
**Two-dimensional mid-domain model consistency**

Observed bird and mammal species richness are unrelated to the predictions of spreading dye 2D mid-domain models in areas of low richness, and they are inversely related in areas of high richness (Fig. 5). The 2D spreading dye model predicts increasing species richness towards the centre of Madagascar. Both bird and mammal endemic species richness are lower near the coast than somewhat

Madagascar, in the area where MDE predictions suggest there should be a peak in richness.

**MDE predictions and range size**

Although the range size frequency distributions of birds and mammals are dissimilar (there are many more broadly



**Figure 5** Scatterplot of observed endemic bird species richness vs. the spreading dye mid-domain prediction of endemic bird species richness per grid cell in Madagascar. The solid line through the data is a LOWESS curve (tension = 0.7). This graph is very similar to that for endemic mammal species richness. To be consistent with MDE predictions, observed richness patterns must, minimally, be positively correlated with spreading dye predictions.

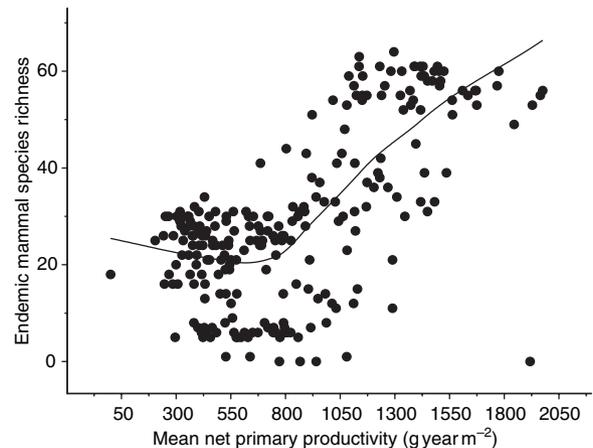
further inland, but richness declines steeply towards the centre of the country (Fig. 2). Minimum richness is found in quadrats near the mid-domain of Madagascar, qualitatively opposite to the pattern predicted by mid-domain models.

### Combined environment–mid-domain model patterns

In contrast to the relationship with MDE predictions, species richness is strongly related to environmental factors (Table 1). For both endemic species assemblages, measures of remaining natural habitat or extent of human-modified lands per quadrat (derived from vegetation sensor observations) are strong predictors of species richness. Quadrats with greater quantities of forested area contain more bird species. Quadrats with less human-modified areas have greater endemic mammal species richness. Species richness also correlates with measurements of primary productivity (Fig. 6), and less strongly with elevation.

## DISCUSSION

Madagascar has been presented (Lees *et al.* 1999) and cited (e.g. Colwell *et al.* 2004; Pimm & Brown 2004) as the most convincing example of a broad-scale gradient of species richness resulting from an MDE. Madagascar does not straddle the equator, so climatic and environmental-gradient hypotheses predict very different patterns of species richness from those predicted from an MDE (i.e. in one



**Figure 6** Net primary productivity ( $\text{g m}^{-2} \text{ year}^{-1}$ ), based on 1-km resolution NOAA14/AVHRR satellite measurements, is a significant predictor of endemic mammal species richness in spatial regression (based on equal-area quadrats;  $n = 228$ ). A LOWESS curve (tension 0.7) illustrates the shape of the NPP–richness relationship. NPP may also provide a sensitive indication of habitat loss.

dimension, climate predicts increasing richness towards the equator while MDEs would have richness increase towards the mid-latitudes of Madagascar).

In contrast, our data on endemic bird and mammal species richness are, at best, only weakly consistent 1D patterns predicted by the mid-domain hypothesis. Richness in  $0.5^\circ$  latitudinal bands is greatest in the mid-latitudes of Madagascar, as Lees *et al.* (1999) note, within the rainforest biome. However, on the island as a whole, latitudinal band area increases sharply towards the mid-latitudes of Madagascar. If differences in the area of latitudinal bands are statistically held constant, the mid-latitude peak of richness disappears (Fig. 4a–c), to be replaced by gradients of increasing species richness towards the equator, just as climate-based hypotheses predict. It is impractical to test hypotheses about environmental controls on 1D patterns of richness because within-band variability in topography, precipitation, land cover and human influences are all large. Consequently, within-band variance of environmental variables would be similar to the among-band variance, and any richness–environment relationships would be obscured (and would violate an assumption of ordinary least-squares regression).

Two-dimensional predictions of mid-domain hypothesis are much more powerful. To the extent that hard boundaries should create an MDE, they should do so in all directions, not just along latitudinal gradients. Two-dimensional gradients are less likely to be collinear with environmental gradients, and they therefore permit concurrent tests of effects of environmental gradients.

Two-dimensional mid-domain models predict a mid-domain peak of richness, whereas the Madagascar bird and mammal data show the opposite: a mid-domain 'valley' of richness. Mid-domain effects are thought to apply only to endemic species (Colwell & Lees 2000); in contrast, Madagascar endemic and non-endemic species richness patterns are very similar (birds: adjusted  $R^2 = 0.508$ ,  $P < 10^{-5}$ ; mammals: adjusted  $R^2 = 0.750$ ,  $P < 10^{-5}$ ), both with mid-domain minima. The most parsimonious explanation of this observation is that similar factors influence both assemblages.

Although 2D variation of species richness is unrelated to mid-domain model predictions, it does relate strongly to contemporary environmental characteristics. Richness is positively related to both remotely sensed estimates of net primary productivity and forest cover. Richness–productivity correlations have been hypothesized to reflect availability of energy or food resources (e.g. H.-Acevedo & Currie 2003; Hurlbert & Haskell 2003; Hawkins *et al.* 2003). Richness is also clearly higher in forested than in non-forested parts of Madagascar, independently of differences in productivity. Wide areas of Madagascar are subject to extensive annual burns that have occurred for decades or centuries (Langrand 1990; Randriambelo *et al.* 1998), creating expanses of low-richness grassland (Lowry *et al.* 1997). Presumably, forested areas provide suitable habitat for more bird and mammal species than frequently burned grassland.

These observations lead to two questions. The impetus for the present study was the finding of a mid-domain peak of richness in Madagascar by Lees *et al.* (1999). Why do our results differ from theirs? Second, is it reasonable to expect to observe an MDE in areas affected by human activities?

### Comparison with Lees *et al.*

Lees *et al.* tabulated two sets of richness data: a 2D grid with quarter-degree cells covering the entire island, and quarter-degree latitudinal bands. They did this for enariine beetles, mycalesine butterflies, non-mycalesine butterflies, frogs, rodents, tenrecs, chameleons, ctenuchiine moths, tiger beetles, lemurs and endemic birds. Although they present data for the entire island, Lees *et al.* restricted their quantitative analysis to a 'fairly uniformly slim north–south belt, the Eastern rainforest biome', and to the species occurring therein.

The island-wide data of Lees *et al.* (1999) show exactly the same pattern we observed: mid-domain minima of richness in all the taxa they studied (their Fig. 8). Central Madagascar is in the rain shadow of the eastern coastal mountains. The dry interior of the island is uniformly less species rich than the coastal rainforest. Because of the climatic variation, there are several biomes in Madagascar, including rainforest,

deciduous forest, thorn forest, etc. (Langrand 1990; Lees *et al.* 1999), and richness clearly varies with climate among biomes.

Lees *et al.* (1999, their Table 4) also showed that richness varies significantly with potential evapotranspiration, precipitation and elevation *within* the rainforest biome. Similar richness–climate relationships, both among and within biomes, have been observed for angiosperms worldwide (Francis and Currie 2003). Within-biome richness–climate relationships are weaker than among-biome relationships because the range of variation of climate within biomes is small relative to the range among biomes. Thus, in these respects, variation of richness within Madagascar rainforest is also consistent with our results.

However, in contrast to their island-wide mid-domain minima of richness, Lees *et al.* report variation of richness within the rainforest biome that is consistent with both 1D and 2D mid-domain models. Consider first their 2D results. As noted above, the rainforest biome is essentially linear, which Lees *et al.* (p. 531) saw as an advantage. To be exact, in their analysis, the rainforest biome averages 4.7 pixels wide, whereas it is 48 pixels long. Lees *et al.* present the predictions of a 2D model; however, not surprisingly, the great majority of the predicted values fall along a smooth function of latitude (their Fig. 11J). Lees *et al.* show no results or model predictions as functions of longitude, presumably because the gradient is too short. Because the domain of the test was essentially 1D, the predicted variation was largely 1D, and the test of fit was essentially a test of 1D variation. In our opinion, the rainforest biome in Madagascar was simply an inappropriate domain to provide a rigorous test of a mid-domain model.

The data of Lees *et al.* do clearly show a 1D mid-domain peak in richness; however, this was almost certainly strongly enhanced by two procedural artefacts. Lees *et al.* (p. 547) note that, 'jaggedness in [their] empirical data is caused by a great irregularity in geographic density and exhaustiveness of sample effort (Fig. 5a,c,e,g)'. First, the capital, the main transportation corridors through the rainforest, and a number of parks and reserves are concentrated in central Madagascar (Langrand 1990, Map 3; Lees *et al.* 1999). Thus, it seems likely that there has been a substantial mid-domain peak in sampling intensity. A more serious problem is interpolation: 'range contiguity is assumed between recorded limits' (p. 535). Lees *et al.* (1999, p. 537) report that 89.4% of their data represented interpolated data between observed presences. Interpolated data necessarily add to observed richness in the middle of the domain, not at the ends. Interpolation applied to a random set of points along a gradient creates an artefactual mid-domain peak of richness (Currie and Kerr, unpublished data). The non-interpolated data of Lees *et al.* (their Fig. 5) do not show an obvious mid-domain peak, especially if questions regarding the dispro-

portionately sampled mid-domain Périnet hot-spot are addressed (as Lees *et al.* do, p. 553). As the vast majority of the data were interpolated, the 1D mid-domain peak in Madagascar may principally reflect a methodological artefact.

### Mid-domain effects in human-modified environments

Would one expect to observe MDEs in a human-modified environment such as Madagascar? The mid-domain hypothesis was proposed to explain broad-scale patterns of species richness (Colwell & Hurtt 1994). Most studies that have examined MDEs have considered large areas such as the Americas (e.g. Willig & Lyons 1998; Bokma *et al.* 2001) or sub-Saharan Africa (Jetz & Rahbek 2001). Yet, these areas have been extensively modified by humans. How much prairie or old-growth forest is left? Sanderson *et al.* (2002) estimated that 83% of the Earth's surface is impacted by human activities. Restricting the mid-domain hypothesis to areas unaffected by human activities would consign it to irrelevance.

Might the biota of extensively modified areas (e.g. much of the interior of Madagascar) have had insufficient time to return to something approaching equilibrium with their environmental conditions, including mid-domain constraints? This seems unlikely. Human activities and climate change have modified environments dramatically throughout the Holocene. Nonetheless, patterns of richness typically relate very strongly to contemporary environmental conditions (Hawkins *et al.* 2003). If richness were strongly out of equilibrium with environmental conditions, the two should not be correlated.

How, then, should MDEs in a world affected by human activities be tested? Colwell *et al.* (2004) sensibly propose that MDEs are one factor among many that potentially may affect geographical patterns of richness. One could hypothesize that MDEs are additive with environmental gradients: i.e. the probability that a species occurs in a particular location is a function of the geometric location within the domain, as well as environmental variables. Human activities may modify environmental variables, and species' distributions respond to the environment (including humans) accordingly. Based on this hypothesis, MDE effects should be detectable in the residuals of richness–environment relationships. In contrast, we found that, after controlling for the environmental gradients with which richness is correlated (NPP and forest cover), there was no detectable MDE signal. This is not because collinearity between MDE predictions and either NPP or forest cover hides their effects ( $r < 0.06$  in all cases). We found no evidence of an MDE as an additive component of influences on richness.

Alternatively, it is possible that species' potential ranges are defined by environmental variables, and MDEs

establish within those domains (e.g. Jetz & Rahbek 2001 treat the Sahara as a domain boundary). This view considerably complicates the interpretation of an MDE as the pattern expected in the absence of environmental gradients. A null hypothesis that controls for environmental variables in order to predict the patterns of richness that would be expected in the absence of environmental gradients is logically precarious. It also risks making the mid-domain hypothesis impossible to operationalize, as definition of domains limits could be species-, environment-, and context-specific. It is possible that patterns of richness may one day prove to be related to some hybrid model that includes an interaction between mid-domain and human effects; however, no such model exists at present.

In sum, Madagascar has been presented as an impressive victory of MDEs (Pimm & Brown 2004). We find that endemic bird and mammal species richness in Madagascar as a whole in fact show the opposite of an MDE. Contemporary environmental characteristics, not mid-domain models, explain most of the variation in patterns of richness. Within a single biome (which serves to control most climatic variation), excluding deforested areas (which controls land cover), Lees *et al.* (1999) observed a latitudinal peak in richness. However, at least two methodological artefacts (sampling intensity and range interpolation across mid-latitudes) may be responsible for even this residual, 1D MDE in Madagascar.

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