

THE EVOLUTION OF LOCAL ENDEMISM IN MADAGASCAR: WATERSHED VERSUS CLIMATIC GRADIENT HYPOTHESES EVALUATED BY NULL BIOGEOGRAPHIC MODELS

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Substantial insular speciation has resulted in exceptionally high levels of endemism in Madagascar, creating locally restricted species' ranges that remain poorly understood. The contributions of alternative processes that could influence patterns of local endemism—including speciation by geographic isolation or adaptation to environmental gradients—are widely debated, both for Madagascar and elsewhere. A recently proposed hypothesis (the “watershed hypothesis”) suggests that allopatric speciation driven by isolation in watersheds during Quaternary climate shifts provides a general explanation for patterns of local endemism across taxa in Madagascar. Here we tested coincidence between species' distributions and areas of endemism predicted by two contrasting biogeographic hypotheses: (1) the watershed hypothesis, and (2) an alternative hypothesis driven by climatic gradients (the “current climate hypothesis”). Statistical significance of coincidence was assessed by comparing against a null model. Surprisingly, we found that extant distributions of lemurs, geckos, and chameleons reveal species patterns that are significantly coincident with the watershed and current climate hypotheses. These results strongly support local endemism developing from multiple processes, even among closely related species. Our findings thus indicate that pluralistic approaches will offer the best option both for understanding processes that generate local endemism, and for incorporating endemism within conservation priority setting.

KEY WORDS: Biogeography, speciation.

The biota of Madagascar has long been recognized for its diversity, with exceptionally high levels of endemism for many biological groups (Myers et al. 2000). Although the long isolation (approximately 80 million years) of Madagascar from all other landmasses (Storey et al. 1995) has contributed to the evolution of diverse terrestrial clades that are endemic to the island, the origins of often spectacular local endemism within the island remain uncertain (Yoder et al. 2005). Several alternative mechanisms may have generated local endemism, including allopatric

speciation driven by isolation (Mayr 1963), for example, due to rivers (Pastorini et al. 2005) or watersheds (Wilmé et al. 2006); parapatric speciation along environmental gradients (Smith et al. 1997; Schneider et al. 1999); or ecologically mediated postspeciation range shifts (Losos and Glor 2003). The relative importance of these competing mechanisms remains widely debated, both for Madagascar and globally.

Patterns in the distribution of Madagascar's unique lemurs have been extensively studied, and the role of rivers as

isolating features has been proposed, at least for some species (Martin 1972; Goodman and Ganzhorn 2004; Pastorini et al. 2005). However, a recent assessment of extant diurnal lemurs has led to a novel hypothesis emphasizing the potential isolation of populations in watersheds with different elevational ranges during periods of climate change (Wilmé et al. 2006). Wilmé et al. (2006) proposed that watersheds with sources at high elevation maintained mesic conditions during Quaternary climate shifts due to orographic precipitation. These retreat–dispersion watersheds may have been used by species retreating from increased aridity at lower elevation, thus isolating populations from lower watersheds and facilitating allopatric speciation (and conversely, resulting in no endemism between the interconnecting higher watersheds). Wilmé et al. (2006) proposed that this mechanism (which we here refer to as the “watershed hypothesis”) explains the explosive speciation and current patterns of local endemism for a significant proportion of Madagascar’s fauna. Allopatric speciation by isolation is therefore invoked as a dominant process providing a general explanation across taxa (Wilmé et al. 2006). However, the watershed hypothesis fails to explain some well-known patterns in the distribution of local endemism across multiple taxa in Madagascar, most notably high montane endemism (Jenkins 1987; Raxworthy and Nussbaum 1994; Raxworthy et al. 2008a,b). This finding has been most recently supported by a detailed study of the cophyline microhylid frog radiation in Madagascar, which exhibits centers of endemism and species richness on the major massifs of the island (Wollenberg et al. 2008). The watershed hypothesis also fails to account for nonconcordant patterns of local endemism among taxa (Kremen et al. 2008).

Concerning the majority of taxonomic groups that are primarily distributed at low and midelevation (< 1500 m) in Madagascar (e.g., lemurs, and most reptile groups), some authors have highlighted the potential importance of climate regimes in generating local endemism. Madagascar has substantial environmental gradients and diverse climates that may play a role in the generation of local endemism (Dewar and Richard 2007). For example, a potential role for parapatric speciation along climatic gradients in the radiation of *Phelsuma* geckos has been discussed by Raxworthy et al. (2007). The interior of the island forms a high plateau above 1000 m elevation, with three major massif systems including summits above 2500 m. The island’s steep eastern escarpment means that much of the rainfall from the Indian Ocean trade winds falls on the eastern side of the island, thus creating a western rain-shadow. Temperatures also vary considerably across the island, with lower seasonal variation in northern Madagascar resulting from the latitudinal range of the island (12–25°) (Donque 1972). We refer to the proposed role of climate patterns in generating local endemism as the “current climate hypothesis.”

These two contrasting speciation hypotheses at low and midelevation should produce very different patterns of local en-

demism, especially in topographically diverse areas where rivers (and hence retreat–dispersal watersheds) flow from high to low elevation, whereas climate gradients tend to run parallel to elevational isolines. Although ecologically mediated postspeciation range shifts might also have been substantial in Madagascar, we assume here that this process would not favor either of these patterns. Indeed conversely, because dispersal is often considered to include elements of stochasticity, this might even be expected to randomize patterns of endemism. The objective of this study was to test for coincidence between areas of endemism (AOEs) predicted by the watershed and current climate hypotheses using species’ distributions of extant diurnal lemurs and three reptile groups: leaf-tailed geckos, day geckos, and chameleons.

Materials and Methods

SPECIES’ OCCURRENCE RECORDS

Occurrence records for *Phelsuma* (day geckos), *Uroplatus* (leaf-tailed geckos), and *Furcifer* (chameleons) were compiled based on voucher specimens held at the American Museum of Natural History and the University of Michigan Museum of Zoology, and supplemented with other records from the literature (occurrence records are included as Supporting Appendix S1). Literature records were evaluated carefully to check species identification and geo-referencing. We follow the taxonomic revision of *Phelsuma* presented in Raxworthy et al. (2007). Distribution data and taxonomy for lemurs were taken directly from Wilmé et al. (2006). Distributions for all species were resampled to a resolution of 1 km², such that duplicate records in the same grid cell were ignored. We excluded from our analyses species known only from one or two grid cells, because sample sizes were too low to construct minimum convex polygons. In cases in which described subspecies appear to warrant recognition as full species, we here treat them as such, but maintain the current taxonomic nomenclature. In total, we included in our analyses 25 lemurs, 21 day geckos, 14 leaf-tailed geckos, and 13 chameleons.

RETREAT–DISPERSION WATERSHEDS

To assess the watershed hypothesis we identified retreat–dispersion watersheds following criteria proposed by Wilmé et al. (2006). Based on an exploration of concordance between watersheds and terrestrial vertebrate endemism, these authors selected retreat–dispersion watersheds as being watersheds of rivers with headwaters above 2000 m. We identified watersheds by delineating drainage systems using the US Geological Survey’s Hydro1k digital elevation model (DEM). The direction of runoff flow for each grid cell was derived from the DEM and the upslope area contributing flow to a given outlet point was calculated. Outlet points were specified as being the mouths of rivers with headwaters above 2000 m, as identified by Wilmé et al. (2006). The drainage

basins of the Antainambalana, Mandrare, and Onilahy rivers that were ambiguously termed as “potential” retreat–dispersion watersheds by Wilmé et al. (2006) were not included in our analyses. To delimit eastern and western watersheds, we calculated flow accumulation (the accumulated weight of all cells flowing into each downslope cell) across the island and identified topographic ridges as comprising those cells with zero accumulation. These analyses were undertaken using the Hydrologic Modeling Tool for ArcMap GIS (ESRI Inc., Redlands, CA). Digital GIS layers for the identified watersheds are included as Supporting Appendix S2.

CLIMATIC CLASSIFICATION

We used cluster analysis to develop a classification of Madagascar’s climate to test the current climate hypothesis. We used 19 bioclimatic variables extracted from the WorldClim database (Hijmans et al. 2005), which is a set of global climate layers generated through interpolation of climate data from weather stations. Weather station data for Madagascar covered the period 1930–1990 and included temperature records from approximately 117 stations (R. Hijmans, pers. com.). The weather stations used were distributed widely across Madagascar, although there is some bias toward lower elevations (Hijmans et al. 2005). As with all analyses presented here, these data were projected to an oblique Mercator equal-area projection at 1 km² resolution. Each of the 19 variables was normalized to the range 0–1 and principal components analysis was used to reduce dimensionality and remove correlation between variables. Following the relative percent variance criterion (McGarigal et al. 2000), we retained the first four principal components, which accounted for 95% of the cumulative variance. Classification of the four principal components was undertaken using unsupervised Iterative Self Organizing clustering and each cell was assigned to a class using maximum likelihood, as implemented in ArcMap GIS (ESRI, Inc.). We defined 14 climate clusters so as to enable direct comparison with the watershed classification, which identified 14 AOE, including two complexes of retreat–dispersion watersheds (one northern and one central/southern) (Wilmé et al. 2006). We treat each of the 14 climate clusters as a potential AOE. Digital GIS layers for the climate clusters are included as Supporting Appendix S3.

NULL MODEL TEST OF COINCIDENCE

To quantify coincidence between species’ distributions and AOE defined by each hypothesis, we drew the minimum convex polygon (MCP) around occurrence records for each species (Supporting Fig. S1; see also Wollenberg et al. 2008) and calculated the percent overlap between the MCP and the AOE. The percent overlap was calculated as $MCP \cap AOE / MCP \cup AOE$. Thus, coincidence (measured as percent overlap) is highest when MCP and AOE are spatially overlapping and are of similar size. For each species, we selected the associated AOE as being that which

incorporated the largest proportion of the MCP. Use of the MCP relieves problems of spatial autocorrelation and sampling bias associated with using point occurrence records (Wollenberg et al. 2008), and despite limitations (Getz and Wilmsers 2004) provides a general depiction of the area inhabited by a species that is useful in the current application.

To test whether coincidence between species’ distributions and AOE was statistically significant, we implemented a null model that generated multiple random distributions. For each species, 10,000 null distributions were created by randomly placing the MCP on the landscape and randomly selecting an orientation (in the current implementation, distributions were rotated in increments of 90° and/or mirrored in either the horizontal or vertical plane). The result was a computer implementation equivalent to randomly casting scale cutouts of the MCP distribution onto a scale map of the study area (Beven et al. 1984). Each null distribution was checked to ensure that all occurrence points fell on land (any null distribution with an occurrence in the sea was rejected), and that the null MCP covered at least as much land area as the true MCP. For each null distribution, percent overlap was calculated following the same procedure as for the true distribution. Statistical significance was then assessed by testing whether the true percent overlap was ranked among the top 5%, 1%, or 0.1% of null distributions, giving three levels of significance: $P < 0.05$, $P < 0.01$, $P < 0.001$. For a few species, distributions were too widespread to enable sufficient random distributions to be generated for the null test (Supporting Table S1). These species (including two lemurs—*Eulemur fulvus* and *E. rufus*—classified as widespread by Wilmé et al. [2006]) were excluded from our analyses because they do not represent restricted-range local endemism.

Results

Patterns of local endemism predicted by the watershed and current climate hypotheses were starkly different (Fig. 1). Differences were most apparent along elevational gradients, where climate clusters delimit areas with similar elevation (including high montane environments) whereas retreat–dispersion watersheds flow down slope and are thus oriented roughly perpendicular to the climate clusters (no montane AOE are recognized using these watersheds). This pattern is especially evident along the eastern escarpment, where climate clusters oriented parallel to elevational isolines along the coast are bisected by retreat–dispersion watersheds flowing from the central (Mangoro) and southern (Manampatrana, Mananara) highlands. The pattern is less evident in the western lowlands, where less-pronounced elevational gradients mean that climate clusters reveal a latitudinal gradient that conflicts less with the AOE predicted by the watershed hypothesis.

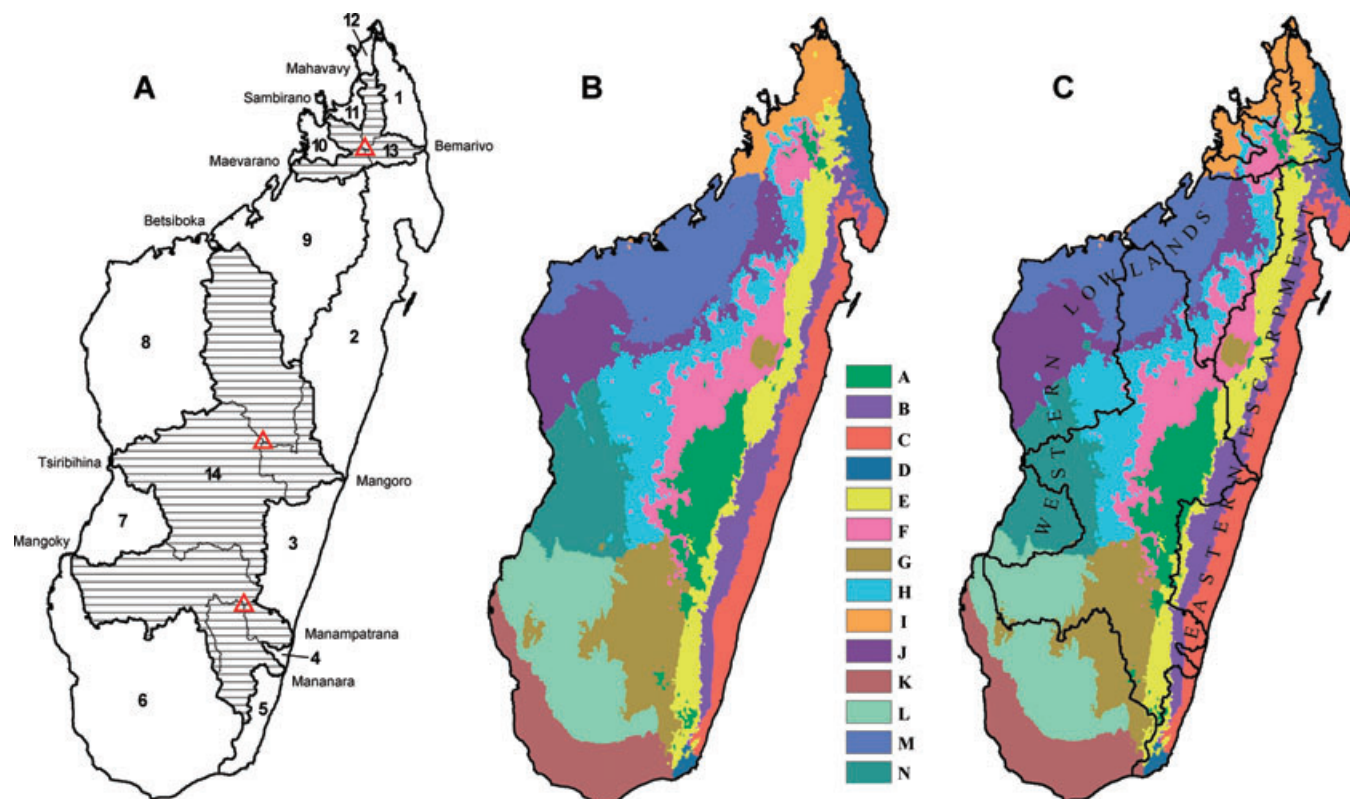


Figure 1. Climate classification and retreat–dispersion watersheds for Madagascar. (A) Retreat–dispersion watersheds, after Wilmé et al. (2006). The retreat–dispersion watersheds delimit 14 areas of endemism, including 12 assemblages of smaller watersheds isolated between retreat–dispersion watersheds (numbered as in Wilmé et al. 2006) and two complexes of interconnected retreat–dispersion watersheds (shaded and numbered 13, 14). Boundaries between watersheds within areas 13 and 14 are drawn with thin black lines. Massifs above 2000 m are labeled with triangular symbols, and major rivers with headwaters above 2000 m are named. (B) Colors show the distributions of 14 climate classes identified by cluster analysis (see Materials and Methods). Climate clusters follow elevational isolines along the eastern escarpment and in the northern, central, and southern highlands; by contrast, clusters reveal a latitudinal gradient in the less topologically diverse western lowlands. (C) Retreat–dispersion watersheds and climate clusters overlaid to show substantial differences, especially along the eastern escarpment (where retreat–dispersion watersheds run down slope and climate clusters are oriented across the slope) and in the highlands (where climate clusters delimit high montane environments whereas retreat–dispersion watersheds connect high and low elevations).

Based on our null model test, across all 73 lemur, gecko, and chameleon species tested we found that 32 species' distributions were significantly coincident ($P < 0.05$) with the watershed hypothesis, and 24 distributions were significantly coincident with the current climate hypothesis (Table 1). Of these cases, 15 species' distributions were significant for both hypotheses, meaning that in total 41 species were significant with one or both hypotheses. Of these 41 species, 20 reached a greater level of significance (based on three levels: $P < 0.05$, $P < 0.01$, $P < 0.001$) for the watershed hypothesis, 15 reached a greater level of significance for the current climate hypothesis, and six reached an equal level of significance for both hypotheses. The remaining 32 species that we tested did not show significant coincidence ($P < 0.05$) with either hypothesis (Fig. 2, and Supporting Table S1). Within all four taxonomic groups assessed, we found species' distributions that were coincident with each of the hypotheses.

Assessing coincidence with each AOE (Fig. 3), we found a relatively even distribution of species across AOE for the watershed hypothesis, which showed significant coincidence ($P < 0.05$) with at least one species in 10 of 14 areas. By contrast, the current climate hypothesis showed significant coincidence with at least one species in 7 of 14 AOE. For the watershed hypothesis, AOE labeled 1 and 2 had the highest numbers of coincident species (6 and 9, respectively), whereas for the current climate hypothesis the area labeled I had the highest number of coincident species with 11.

Discussion

By applying a null biogeographic model, our results show that patterns of endemism in Madagascar are consistent with multiple potential driving mechanisms, thus cautioning against a “one

Table 1. Coincidence between species' distributions and areas of endemism predicted by the watershed and current climate hypotheses.

Species	<i>n</i> ¹	Watershed hypothesis			Current climate hypotheses		
		Percent overlap ²	Significance ³	AOE ⁴	Percent overlap ²	Significance ³	AOE ⁴
Lemurs:							
<i>Eulemur coronatus</i>	17	65.4	***	1	21.4	*	I
<i>E. albifrons</i>	48	69.3	***	2	36.3	*	C
<i>E. sanfordi</i>	10	9.3	*	1	10.8	**	I
<i>E. m. flavifrons</i>	10	16.8	**	10	9.2	**	I
<i>E. m. macaco</i>	16	28.3	*	10	20.5	**	I
<i>Indri indri</i>	59	62.6	***	2	26.7		
<i>Lemur catta</i>	128	53.2	*	6	38.1	***	L
<i>M. griseorufus</i>	21	48.9	**	6	38.9		
<i>M. tavaratra</i>	6	0.2			0.2	*	I
<i>Propithecus diadema</i>	24	33.8	*	2	23.4		
<i>P. edwardsi</i>	32	66.3	***	3	25.3		
<i>P. perrieri</i>	6	1.8	*	1	1.0	*	I
<i>P. tattersalli</i>	8	6.1	*	1	2.3	*	I
<i>P. deckeni</i>	52	61.7	**	8	40.2		
<i>P. verreauxi</i>	108	46.7			35.4	***	L
<i>V. variegata</i>	52	43.2	**	2	29.3		
Day Geckos:							
<i>Phelsuma abbotti</i>	19	23.3			39.4	*	M
<i>P. antanosy</i>	4	2.6	*	5	2.0	**	D
<i>P. barbouri</i>	10	3.5			18.1	***	A
<i>P. berghofi</i>	4	4.6	**	5	1.6		
<i>P. breviceps</i>	10	14.1			34.3	***	K
<i>P. dubia</i>	12	16.0			48.0	*	M
<i>P. guttata</i>	18	40.6	*	2	16.2		
<i>P. hielscheri</i>	3	22.8	*	7	10.8		
<i>P. kochi</i>	20	67.3	***	8	32.6		
<i>P. laticauda</i>	18	41.0	*	13	20.9		
<i>P. madagascariensis</i>	13	27.1			59.3	***	C
<i>P. modesta</i>	26	34.7			42.9	*	K
<i>P. pusilla</i>	15	45.0	**	2	49.5	***	C
<i>P. quadriocellata</i>	24	38.5	**	2	34.1		
<i>P. seippi</i>	7	15.6	*	10	9.1	*	I
Leaf-tailed Geckos:							
<i>Uroplatus alluaudi</i>	3	0.19	**	12	0.02	*	I
<i>U. sp. 4</i>	5	18.9	*	13	5.0		
<i>U. fimbriatus</i>	15	50.0	***	2	26.6		
<i>U. guentheri</i>	7	45.2	*	8	17.8		
<i>U. sameiti</i>	16	38.5	*	2	47.6	***	C
<i>U. sp. 8</i>	6	25.8	**	1	10.4	**	I
<i>U. sp. 2</i>	4	0.6	**	12	0.03		
Chameleons:							
<i>Furcifer campani</i>	6	5.8			26.1	**	A
<i>F. petteri</i>	6	17.8	**	1	10.8	**	I
<i>F. verrucosus</i>	65	77.0	***	6	33.9		

¹Number of occurrence records.²Percent overlap between species' distribution and area of endemism (see Materials and Methods).³Statistical significance compared against a null model, to three levels of confidence: ****P* < 0.001, ***P* < 0.01, **P* < 0.05. Only species with significant coincidence for at least one of the hypotheses are shown here (results for all species assessed are presented in Supporting Table S1).⁴Area of endemism with which the species' distribution is coincident (labels as in Fig. 1).

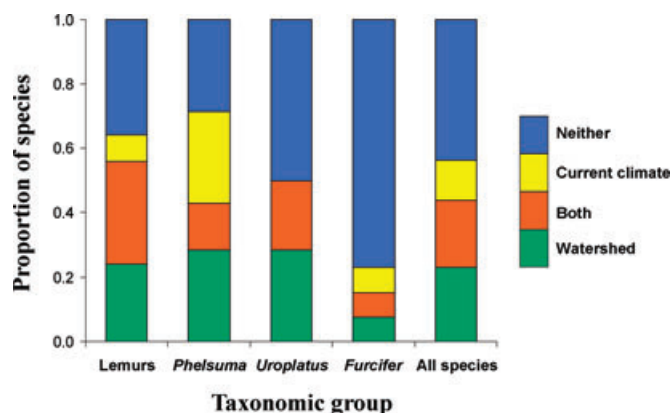


Figure 2. Proportion of species' distributions that are coincident with areas of endemism predicted by alternative hypotheses. Results are for 25 species of lemurs, 21 species of *Phelsuma* geckos, 14 species of *Uroplatus* geckos, and 13 species of *Furcifer* chameleons (see Supporting Table S1). Bars show the proportion of species' distributions that are coincident with areas of endemism predicted exclusively by the current climate hypothesis, exclusively by the watershed hypothesis, by both hypotheses, or by neither hypothesis. A species' distribution was classified as coincident if overlap with a predicted area of endemism was significantly better than expected compared against a null model ($P < 0.05$). Within each taxonomic group, there are species coincident with each hypothesis.

size fits all" approach to explaining endemism across multiple groups, or even among closely related species. By analyzing four taxonomic groups that are primarily distributed across low and midelevations, our analyses build upon a recent assessment of cophyline microhylid frogs (which are primarily restricted to higher elevations) that found little support for the watershed hypothesis for this group (Wollenberg et al. 2008).

The two hypotheses that we tested link closely with alternative speciation processes. Our analyses support Pastorini et al. (2005) and Wilmé et al. (2006) in noting the importance of some major rivers (including Betsiboka and Mangoro), and their retreat–dispersion watersheds, as isolating barriers for lemurs, potentially driving allopatric speciation. These findings suggest that for about half the diurnal lemur species, major rivers represented substantial barriers to dispersal and changing distributions of gallery forest in watersheds (as a result of climate change) created isolated refugia, which together have provided opportunities for allopatric speciation.

However, many species' distribution limits do not correspond to the largest river systems; for example, many reptile distributions straddle major rivers and are instead restricted to elevational bands (Raxworthy et al. 2008a,b). We found that a high proportion of *Phelsuma* day gecko distributions were coincident with AOE predicted by the current climate hypothesis, which supports Raxworthy et al.'s (2007) suggestion that parapatric specia-

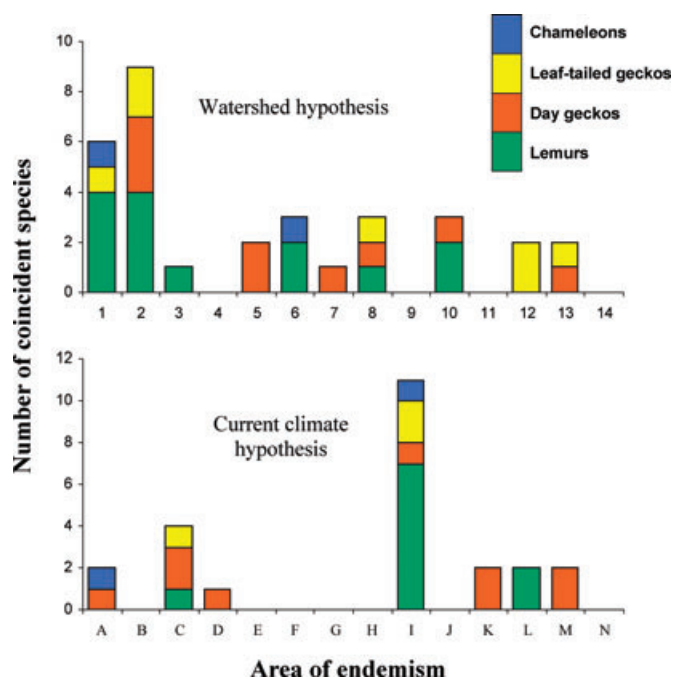


Figure 3. Number of species' distributions that are coincident with each area of endemism predicted by the watershed and current climate hypotheses. A species' distribution was classified as coincident if overlap with a predicted area of endemism was significantly better than expected compared against a null model ($P < 0.05$). Areas of endemism are identified by numbers and letters as in Figure 1. Results show a relatively more even distribution of species across different areas of endemism for the watershed hypothesis.

tion along environmental gradients offers the most parsimonious explanation for local endemism among some *Phelsuma* geckos. These geckos are not heavily dependent on riverine or gallery forests (C. J. Raxworthy, pers. obs.) and thus isolation in lower watersheds (as per the watershed hypothesis) may have been less severe for this group. This is particularly striking for the climate hypothesis area C (East coast), where three geckos had highly significant coincident distributions ($P < 0.001$, Table 1) that are utterly at odds with the watershed hypothesis.

For the other two reptile groups, *Uroplatus* and *Furcifer*, the majority of species do not show coincident patterns of endemism with either watershed or climate clusters. Like *Phelsuma*, these groups are not dependent on gallery forest, but unlike *Phelsuma*, the climate clusters that we used provide a poor fit to their patterns of endemism. We suspect for both groups that other environmental variables (beyond the WorldClim precipitation and temperatures variables) could have influenced patterns of endemism, or else, that speciation has resulted from very different drivers. The exceptionally poor coincidence we find in *Furcifer* chameleons is especially intriguing. Although highly speculative at this point, there is the potential for sexual selection driving speciation within

this group (Lande 1981), because these lizards show substantial sexual dimorphism and complex courtships displays that provide rich opportunities for mate choice (Karsten et al., in press).

Overall, our results suggest a role for multiple speciation mechanisms, including speciation by geographic isolation or adaptation along environmental gradients, in generating local endemism across multiple taxonomic groups for Madagascar's forest biota. Other studies supporting multiple speciation mechanisms have been reported for taxonomic groups outside Madagascar (e.g., Barroclough and Vogler 2000; Moritz et al. 2000; Coyne and Orr 2004; Kozak and Wiens 2006; Carstens and Knowles 2007). Of particular note though, we find contrasting patterns of endemism within each of our four study groups, even between closely related species of *Eulemur*, *Propithecus*, *Microcebus*, *Phelsuma*, *Uroplatus*, and *Furcifer* (see Pastorini et al. 2005; Raxworthy et al. 2002, 2007, 2008a,b). This biogeographic complexity thus suggests that highly congruent vicariant patterns are unlikely to be recovered in Madagascar.

We note, however, that our analyses cannot distinguish whether current species distributions reflect the original geography of speciation or ecologically mediated postspeciation range shifts (Losos and Glor 2003). Arguably, the incongruent endemism patterns that we report here for these four taxonomic groups could also be the product of substantial postspeciation range changes. However, recent phylogenetic studies in Madagascar are recovering a general trend for sister species to be found in parapatry, or allopatry with sisters separated by modest geographic distance (e.g., Yoder et al. 2000; Olsen et al. 2004; Pastorini et al. 2005; Goodman et al. 2006; Raxworthy et al. 2007, 2008a,b; Wollenberg et al. 2008). These findings thus suggest that current distribution patterns are maintaining a signal that at least partly reflects the original geography of speciation. It also appears that dispersal is geographically highly constrained for these taxonomic groups in Madagascar. Almost all species included in this study are endemic to a relatively small region of the island, with the majority of species occupying less than 25% of Madagascar's surface area. Dispersal constraints may also be evident for species that have established populations outside their natural range within Madagascar, as a result of recent human accidental release. For example, the day geckos *Phelsuma laticauda* and *P. grandis* have recently established new populations around Tamatave and Ivoloïna, 250 km south of their natural range, after escaping from a captive breeding facility (K. Freeman, pers. com.). Local conditions in the Tamatave region appear well suited to these introduced species, which previously were isolated in northern Madagascar, probably by suboptimal habitat and topography (C. J. Raxworthy, pers. obs.).

Across all groups, the overall high proportion of species that were not coincident with either hypothesis (44%) may also be explained by the fact that we do not expect to have captured all

the important driving mechanisms; additional factors, such as the role of habitat history (Graham et al. 2006), may predict patterns of endemism coincident with species' distributions that were not well predicted by either of the hypotheses tested here. The high degree of anthropogenic forest loss in Madagascar (Achard et al. 2002), which causes declines in species' distributions, might also partly account for low coincidence between predicted AOE's and distributions for some species. Similarly, our ability to evaluate biogeographic patterns is limited by the fact that Madagascar's fauna remains relatively poorly known, with many species having relatively few known occurrence records (Supporting Table S1). Our use of MCPs to define species' distributions helps to alleviate the effects of limited sampling (in that species are assumed to occur in areas between known occurrences, Wollenberg et al. 2008), but we also recognize that these polygons represent only an approximation of the actual species' distributions.

We also note that, although rivers and watersheds delimit rigid boundaries between predicted AOE's, the precise distribution (but not general pattern) of climate clustering is dependent on the number of clusters generated (set here at 14 to match the watershed hypothesis), so coincidence between climate clusters and species' distributions might be further optimized. Accuracy of the climate clusters may also be enhanced if improved climate surfaces can be generated using more weather stations that include more high elevation records. With these factors in mind, it is impressive that AOE's predicted by the climate clusters showed highly significant coincidence with many species' distributions. In particular, climate cluster 1 (Fig. 1), which distinguishes the climate in northwestern Madagascar (approximating the Sambi-rano region, as recognized by Humbert 1955), provides a better explanation of local endemism in this region than the watershed endemism areas (see Fig. 1, areas 10–12). By contrast, we suspect that the climatic clusters on the eastern escarpment of Madagascar (areas B, E, and F) may have identified elevational bands that are too narrow to be coincident for most species distributions: we found no species to be significantly coincident with these areas, although midelevation endemism on the eastern escarpment is well known among reptiles (Raxworthy and Nussbaum 1997).

It is also the case that the criteria used to define retreat–dispersion watersheds may be further optimized to increase coincidence with species' distributions. Here we used the criteria that headwaters must exceed 2000 m, as proposed by Wilmé et al. (2006), but the potential role of other, lower watersheds warrants further investigation.

An improved understanding of the mechanisms that generate local endemism, in Madagascar and elsewhere, has important implications for conservation prioritization. In Madagascar, the current expansion phase of the protected areas network by threefold adds particular urgency to improving our understanding of patterns of local endemism on the island (IUCN 2005;

ONE 2006). Wilmé et al. (2006) proposed that AOE defined by retreat–dispersion watersheds should be given conservation prioritization, whereas other initiatives have identified priorities using species distribution models that assume a primary role for current climate in delimiting AOE (Kremen et al. 2008). Our analyses suggest that multiple biogeographic criteria must be built into reserve planning methodologies if the island's exceptional biological diversity and diverse evolutionary processes are to be conserved. This will be especially critical for those regions of Madagascar where we currently have the poorest information on species distributions.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Example species' distributions overlaid on climate clusters and retreat–dispersion watersheds.

Table S1. Coincidence between species' distributions and predicted areas of endemism for all species assessed.

Appendix S1. Occurrence records and specimen details for geckos and chameleons used in the analysis.

Appendix S2. Digital GIS layer (GeoTiff format) for the retreat–dispersion watersheds.

Appendix S3. Digital GIS layer (GeoTiff format) for the climate clusters.

Supporting Information may be found in the online version of this article.

(This link will take you to the article abstract).

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