Ecological divergence and speciation between lemur (*Eulemur*) sister species in Madagascar

M. E. BLAIR*, E. J. STERLING*, M. DUSCH†, C. J. RAXWORTHY‡ & R. G. PEARSON*

*Center for Biodiversity and Conservation, American Museum of Natural History, New York, NY, USA
†College of Environmental Science and Forestry, State University of New York, Syracuse, NY, USA
‡Department of Herpetology, American Museum of Natural History, New York, NY, USA

Abstract

Understanding ecological niche evolution over evolutionary timescales is crucial to elucidating the biogeographic history of organisms. Here, we used, for the first time, climate-based ecological niche models (ENMs) to test hypotheses about ecological divergence and speciation processes between sister species pairs of lemurs (genus *Eulemur)* in Madagascar. We produced ENMs for eight species, all of which had significant validation support. Among the four sister species pairs, we found nonequivalent niches between sisters, varying degrees of niche overlap in ecological and geographic space, and support for multiple divergence processes. Specifically, three sister-pair comparisons supported the null model that niches are no more divergent than the available background region. These findings are consistent with an allopatric speciation model, and for two sister pairs (*E. collaris–E. cinereiceps* and *E. rufus–E. rufifrons*), a riverine barrier has been previously proposed for driving allopatric speciation. However, for the fourth sister pair *E. flavifrons–E. macaco*, we found support for significant niche divergence, and consistent with their parapatric distribution on an ecotone and the lack of obvious geographic barriers, these findings most strongly support a parapatric model of speciation. These analyses thus suggest that various speciation processes have led to diversification among closely related *Eulemur* species.

Introduction

Studies of the degree to which ecological niches change over evolutionary timescales are crucial for understanding how and when environmental factors can influence natural selection (Wiens, 2004; Hickerson *et al.*, 2010; Wiens *et al.*, 2010; MacColl, 2011). In recent decades, a wide range of approaches to construct quantitative models of species' ecological niches have been developed, commonly termed ecological niche models (ENMs) (Franklin, 2009; Peterson *et al.*, 2011), yet researchers are only beginning to explore niche evolution rigorously under these frameworks (e.g. Warren *et al.*, 2008).

Correspondence: Mary E. Blair, Richard G. Pearson, Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th St, New York, NY 10024, USA.
Tel.: (212) 769-5742; fax (212) 769-5292;
e-mails: mblair1@amnh.org, pearson@amnh.org

In this study, we use ENMs to test hypotheses about ecological divergence and speciation processes in the 'true' lemurs (genus *Eulemur* Simons & Rumpler, 1988). *Eulemur* taxa are widespread across natural habitats in Madagascar and exhibit substantial ecological and behavioural flexibility. For sister taxa within *Eulemur* (defined as species that are the only descendants of a common ancestral species; Fig. 1), we explore the processes that may have led to divergence by testing for ecological niche divergence or conservatism. We define ecological niche divergence as the tendency for related species to differ more ecologically than expected by random drift (or simple Brownian motion descent with modification, Losos, 2008). Conversely, we define ecological niche conservatism as the tendency for related species to differ less ecologically than expected by random drift. Here, we test for ecological niche divergence or conservatism using the null model developed by Warren *et al.* (2008), in which observed niche overlap
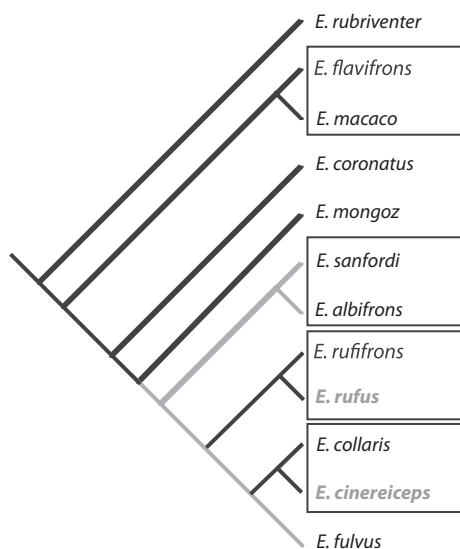
Fig. 1 Molecular-based phylogenetic tree of Horvath *et al.* (2008), with additional taxa (shown in grey) based on the congruent results of Wyner *et al.* (1999), Pastorini *et al.* (2003), Johnson *et al.* (2008) and Gudde *et al.* (2013). Nodes with bootstrap support or clade credibility values < 85% shown in grey, and boxes are drawn around sister species pairs tested in this study.

is compared to a null distribution of overlap values generated from random points within the geographic range of the species pair.

Allopatric speciation is essentially a spatial process whereby two populations become genetically isolated due to geography. This spatial isolation may be facilitated by ecological niche conservatism, because failure to adapt to new environments maintains separation between populations (Wiens, 2004). We therefore hypothesize that allopatric speciation would be supported by a finding of niche conservatism (Wiens, 2004) or a failure to reject a null model such as that of Warren *et al.* (2008) (see Losos, 2008). By contrast, we hypothesize that parapatric ecological speciation on an ecotone could be supported by the finding of ecological niche divergence in combination with additional evidence including parapatric distribution along an ecotone, because this process requires adaptation to different niches (Schneider *et al.*, 1999; Moritz *et al.*, 2000). We also hypothesize that sister taxa showing niche divergence will have smaller geographic distances between their occurrence records, because they could have parapatric speciation history. Post-speciation range shifts may obscure such patterns (Losos & Glor, 2003) as might post-speciation ecological divergence (Graham *et al.*, 2004; Swenson, 2008), yet recent analyses suggest that current species' distributions in Madagascar at least partly reflect the original geography of speciation (Pearson & Raxworthy, 2009). We focus exclusively on sister species pairs within *Eulemur*, to (i) include the

minimal divergence time since speciation to minimize potential post-speciation range shifts and ecological divergence and (ii) avoid the necessity of creating hypothetical ancestral niches for sister lineages.

Multiple hypotheses have been proposed to explain current distributions and biogeographic histories of *Eulemur* taxa. Most invoke allopatric speciation as the dominant evolutionary process behind diversification. For example, Tattersall (1982) hypothesized that taxa in the *E. fulvus* (E. Geoffroy, 1796) group diverged in allopatry following fluctuating periods of increased aridity in the late Pleistocene and Holocene, with forests contracting into isolated refugia (see Gasse & Van Campo, 1998, 2001) and post-isolation migration routes limited by the central plateau and by rivers. Recent studies have evaluated rivers as potential allopatric barriers using genetic data (Pastorini *et al.*, 2003) and by comparing the elevational ranges of lemur species to the elevation of river headwaters (Goodman & Ganzhorn, 2004). Both studies found support for some rivers as potential barriers, but not others: genetic data support the Betsiboka and Tsiribihina rivers as barriers, but not the Mahavavy River; elevational ranges support the Mananara River as a barrier between *E. collaris* (E. Geoffroy, 1796) and *E. cinereiceps* (A. Grandidier & Milne Edwards, 1890), but do not support other rivers as barriers (the Tsiribihina River was not evaluated).

In *Eulemur*, there appears to be a north–south zonation where eastern and western taxa are more similar to one another and are often more closely related than neighbouring populations to the north or south (Ganzhorn *et al.*, 2006). This east-to-west similarity among *Eulemur* taxa has been attributed to the direction of drainage systems, with riverine forests serving as corridors and probably refugia during Pleistocene drought (Maeve & Kellman, 1994; Ganzhorn *et al.*, 2006). The 'watershed hypothesis' (Wilmé *et al.*, 2006) describes a similar scenario for allopatric divergence of several taxa across Madagascar, whereby allopatry would have been established by isolated low-elevation watersheds that maintained mesic conditions during Quaternary climate shifts (Wilmé *et al.*, 2006). There is evidence that some lemur taxa are restricted to watersheds, but for others, distribution breaks do not correspond to watersheds and are instead coincident with climatic zones (Pearson & Raxworthy, 2009). Coincidence between species' distributions and climatic zones has been suggested to be indicative of ecologically mediated speciation (Smith *et al.*, 1997; Schneider *et al.*, 1999; Moritz *et al.*, 2000).

Similarly, Pastorini *et al.* (2003) found phylogenetic evidence supporting a set of biogeographical zones for lemurs in Madagascar (Martin, 1972, 1995), some of which are separated by distinctive climatic characteristics, whereas others are delimited by physical barriers. Overall, the diverse results of studies to date suggest that patterns of endemism among lemurs developed

from multiple processes and that pluralistic approaches are likely to offer the best option for understanding the processes that generate diversification (Pearson & Raxworthy, 2009).

Species delineation and the inference of phylogenetic relationships among *Eulemur* taxa have proven difficult and controversial, largely due to weak phylogenetic signal as a result of short internal branch lengths (Yoder & Irwin, 1999), and also extensive morphological variation. For example, pelage patterns are not completely fixed among putative taxa (Tattersall, 1982). Also, considerable natural hybridization exists among even the more distantly related taxa within the genus (e.g. Wyner *et al.*, 2002; Pastorini *et al.*, 2009). Hybridization is not uncommon in primate lineages with rapid diversification and overlapping or adjacent geographic distributions (Roos *et al.*, 2011; Zinner *et al.*, 2011), making taxonomic and phylogenetic inference challenging.

There is little disagreement about the status of distinct species among the more basal taxa within *Eulemur* (*E. coronatus* Gray, 1842; *E. mongoz* Linnaeus, 1766; *E. rubriventer* I. Geoffroy, 1850; Groves, 2001). The *E. flavifrons–E. macaco* clade also has been consistently supported by phylogenetic analyses (Wyner *et al.*, 1999; Yoder & Irwin, 1999; Pastorini *et al.*, 2003; Horvath *et al.*, 2008; Johnson *et al.*, 2008). However, there is conflicting evidence regarding the phylogenetic relationships between these species and others within the genus due to short internal branch lengths and weak phylogenetic signal (Yoder & Irwin, 1999; Fig. S1). The *E. fulvus* species complex (brown lemurs) has emerged as perhaps the most challenging for taxonomic and phylogenetic inference within *Eulemur* (Table S1, Fig. S1). Until recently, the polytomy of *E. albifrons–E. fulvus–E. sanfordi* had not been resolved, likely because of the recent divergence of the brown lemur complex from the rest of *Eulemur* at around 2.3–4.0 Mya (Horvath *et al.*, 2008). However, Horvath *et al.* (2008) and Gudde *et al.* (2013) showed *E. sanfordi* and *E. albifrons* as sister taxa within this group (Fig. 1). Although the identification of sister taxa is consistent across studies (Fig. S1), basal phylogenetic relationships are not yet resolved in the *E. fulvus* group (Horvath *et al.*, 2008; Johnson *et al.*, 2008; Gudde *et al.*, 2013; Fig. S1). For the purposes of this study, it is important that we can reasonably infer sister relationships of species pairs, but not necessarily the more basal phylogenetic relationships within the group.

Here, we investigate ecological niche conservatism and divergence between four sister species pairs (*E. albifrons–E. sanfordi*, *E. collaris–E. cinereiceps*, *E. flavifrons–E. macaco* and *E. rufus– E. rufifrons*; Fig. 1), to test speciation processes within this group, as well as to provide new ecological evidence to evaluate the currently proposed species taxonomy (Wiens & Graham, 2005; Raxworthy *et al.*, 2007; Rissler & Apodaca, 2007).

Materials and methods

Distribution data for lemurs were taken from Wilmé *et al.* (2006) and modified based on recent studies as follows: All localities labelled *E. rufus* that were south of the Tsiribihina River or on the eastern coast of Madagascar were relabelled as *E. rufifrons* (Pastorini *et al.*, 2003; Ganzhorn & Randriamanalina, 2004; Groves, 2006). Two localities north of the Mananara River were classified as *E. collaris* in Wilmé *et al.* (2006) (latitude S, longitude E: 22 : 09 : 48, 47 : 02 : 30; 22 : 08 : 58, 47 : 01 : 25) but were noted as probably *E. cinereiceps* in the original data source (Goodman *et al.*, 2001); to be conservative, we removed these points. We also removed one locality (latitude S, longitude E: 18 : 05 : 00, 48 : 45 : 00) from *E. rufifrons* dated 1916 from the Parc Botanique et Zoologique Tsimbazaza collection that is well outside the known range (IUCN, 2012). We were ultimately able to include at least 10 and up to 86 occurrence records for each target species, which reasonably reflect their known ranges (IUCN, 2012; Table 1; Table S2).

We constructed ENMs using climate data from the WorldClim database (Hijmans *et al.*, 2005). Modelling was conducted using layers at 30-arc-second (approximately 1-km) resolution, and all analyses were carried out using an Oblique Mercator Projection. Based on reasoning as to the physiological and life history requirements of lemurs and an analysis of correlations between variables in Madagascar, we reduced nineteen commonly used bioclimatic variables to six variables. Two of the six variables represented annual temperature trends (isothermality and temperature annual range), two represented the cold extremes of the year (temperature seasonality and minimum temperature of the coldest month), and one variable represented drought incidence (precipitation of the driest quarter). We expect that cold extremes and droughts may be related to higher infant mortality in lemurs (Wright, 1999; Richard *et al.*, 2000; Dewar & Richard, 2007; Lawler *et al.*, 2009). We also included a variable representing possible occurrence of frost (precipitation of the coldest quarter) because frost contributes to the inconsistent annual fruiting of flora in Madagascar, which is associated with a reduction in food resources (Wright, 1999). Selected variables were not strongly correlated in Madagascar (absolute value of correlations ranged from 0.001 to 0.67, median: 0.25).

We built ENMs using Maxent (software version 3.3.3e, Phillips *et al.*, 2006). Maxent estimates the unknown probability distribution defining a species' range from incomplete information by finding the probability distribution of maximum entropy (that which is closest to uniform) subject to constraints imposed by the known range of the species and environmental conditions across the study area (Phillips *et al.*, 2004, 2006). This approach to niche modelling has been

Table 1 Predictive ability of Maxent models across 4-fold validation (range of AUC across 4-folds, and the omission error and *P*-value of the binomial test for each fold).

Species	N*	AUC†	Omission error (MTP‡)			
			Fold 1	Fold 2	Fold 3	Fold 4
E. albifrons	48	0.930–0.980	0.091, *P* < 0.0001	0, *P* < 0.0001	0, *P* < 0.0001	0, *P* < 0.0001
E. cinereiceps	10	0.902–0.962	0.333, *P* = 0.028	0, *P* = 0.015	0, *P* = 0.017	0, *P* = 0.008
E. collaris	19	0.877–0.904	0, *P* = 0.0008	0.5, *P* = 0.049	0, *P* = 0.0008	0, *P* = 0.0005
E. flavifrons	10	0.992–0.998	0.333, *P* = 0.0003	0.333, *P* = 0.0003	0, *P* = 0.0002	0, *P* = 0.0002
E. macaco	16	0.975–0.992	0.250, *P* = 0.0003	0, *P* < 0.0001	0, *P* < 0.0001	0, *P* < 0.0001
E. rufifrons	86	0.846–0.903	0.143, *P* < 0.0001	0, *P* < 0.0001	0, *P* < 0.0001	0, *P* < 0.0001
E. rufus	33	0.933–0.951	0, *P* < 0.0001	0.125, *P* < 0.0001	0, *P* < 0.0001	0, *P* < 0.0001
E. sanfordi	10	0.962–0.987	0.333, *P* = 0.003	0, *P* < 0.0001	0, *P* = 0.002	1.0, *P* = 1.0

*N = Number of localities used to build model.
†Area under the curve (AUC) = highest area under the receiver-operating characteristic curve.
‡MTP = Under a minimum training presence threshold.

shown to perform well when compared to other methods (Elith *et al.*, 2006). Regularization parameters for each species were selected by testing a range of values from 1 to 10 and determining which model resulted in the highest area under the curve (AUC) of the receiver-operating characteristic plot, calculated using 25% of occurrence points set aside as test data. AUC values range from 0.5 for models with no predictive ability (predictions no better than random) to 1.0 for models giving perfect predictions (Fielding & Bell, 1997; Pearce & Ferrier, 2000). This resulted in regularization parameters equal to 1 for all species. Other model parameterizations (convergence threshold, maximum number of iterations and feature selection) followed generic recommendations by the model developers (Phillips *et al.*, 2006; Phillips & Dudik, 2008).

The predictive capabilities of the models were evaluated using 4-fold partitioning (Peterson *et al.*, 2011). For each fold, we calculated the AUC as described above, which provides a measure of model performance that does not require setting a threshold of occurrence for converting continuous model output into binary predictions of presence and absence. We also calculated the omission rate for each fold by generating binary predictions using a minimum training threshold (Pearson *et al.*, 2007) and used a binomial test to assess whether the observed omission rate was better than expected compared to a random prediction (Anderson *et al.*, 2002).

Niche overlap values for sister taxa were calculated from Maxent models using Schoener's *D* (Schoener, 1968) and Hellinger's *I* niche similarity metrics, as implemented in ENMtools (Warren *et al.*, 2008). These indices quantify predicted niche similarity, which ranges from 0 (no overlap) to 1 (identical niche models).

We used the 'background test' in ENMtools to test for niche conservatism or divergence that cannot be explained by regional similarities or differences in the

habitat available to each species. This test compares the observed niche overlap values to a null distribution of 100 overlap values created by comparing an ENM of one species (Species A) to an ENM generated from random points within the geographic range of the other species (Species B). We also repeated in the opposite direction, comparing an ENM of Species B to an ENM generated from random points within the range of Species A. We defined the geographic range of each species by a minimum convex hull drawn around known occurrence localities (Warren *et al.*, 2010). The number of random points drawn from within each minimum convex hull was equal to the number of original occurrence records multiplied by 100 (Warren *et al.*, 2010). Using a two-sided test and an alpha level of 0.05, we determined whether the overlap value between two ENMs was above the 95% confidence interval of the null hypothesis, supporting niche conservatism, or below the 95% confidence interval of the null hypothesis, supporting niche divergence. If the null hypothesis is supported, then the amount of niche overlap or the lack thereof can be explained by regional similarities or differences in the habitat available to each species. If the background test is significant in one direction, but not the other (e.g. only for Species A against background of Species B, but not for Species B against background of Species A), we took a conservative interpretation and considered this result support for the null hypothesis.

We also used the 'identity test' in ENMtools to test whether the ENMs produced by the two species are equivalent to one another (Warren *et al.*, 2008). In contrast to the 'background test', this test compares the observed niche overlap values to a null distribution of 100 overlap values generated by pooling the point localities for both species, randomizing the species identities of the localities and creating two new samples of the same sizes as the original samples, without consideration of regional similarities or differences in the

habitat available to either species. Observed niche overlap values were compared to the null distribution of the pseudo-replicate niche overlap values using a one-sided test and an alpha level of 0.05. If the observed overlap value fell within the bottom 5% of the null distribution, then we inferred that the two species' ENMs were not equivalent.

To address our hypothesis that sister taxa showing divergence will have parapatric distributions, we measured two types of geographic distances between species' occurrence records. First, we identified weighted centroids from the occurrence records for each species using ArcMap 10 (ESRI; Redlands, CA, USA) and then measured the geographic distance between centroids of sister pairs. Second, we calculated the minimum distance between occurrence records from pairs of species. A minimum distance of zero means that both species were recorded within the same cell at least once.

Results

All eight species' Maxent models showed strong ability to predict observed distributions, with AUC values > 0.84 and significant binomial tests (range of AUC values, 0.846–0.998; omission error, 0–0.5 at $P < 0.05$; see Table 1 for all statistics). The only failed binomial test was for one of four-folds of *E. sanfordi* (AUC: 0.962–0.987, omission error: 0–1.0, three significant binomial tests at $P < 0.01$ and one nonsignificant test at $P = 1.0$, Table 1), a geographically restricted species for which we only had a small number ($N = 10$) of occurrence records.

All species pairs tested were found to have nonequivalent ENMs (Table 2), and pairs showed varying degrees of niche overlap in ecological and geographic space. *Eulemur collaris–E. cinereiceps* showed a large amount of spatial overlap in their ENMs and the highest I and D niche overlap values (Table 2, Fig. 2). *Eulemur rufus–E. rufifrons* showed no spatial overlap in their ENMs and also had the lowest I and D niche overlap values (Table 2, Fig. 3).

Eulemur albifrons–E. sanfordi showed a small area of spatial overlap in their ENMs in the region between Vohemar and Sambava and had the second-lowest I and D niche overlap values (Table 2, Fig. 4). *Eulemur flavifrons–E. macaco* showed a small area of spatial overlap near Maromandia and had the second-highest I and D niche overlap values (Table 2, Fig. 5).

Our sample size was not large enough to test for statistically significant differences between the minimum (MD) and centroid distances (CD) between occurrence points, but MD and CD were the smallest between *E. flavifrons–E. macaco* (MD = 0.0 km, CD = 94.5 km; Table 2). For the other three species pairs, MD ranged from 72.9 to 126.7 km and CD from 221.1 to 506.6 km (Table 2).

In the background test, the null hypothesis was not rejected for *E. albifrons–E. sanfordi, E. collaris–E. cinereiceps* or *E. rufus–E. rufifrons*, meaning that the amount of niche divergence between the pairs of ENMs could be explained by the variability in the available habitat (Table 2, Fig. 2–5). For *E. flavifrons– E. macaco*, the null hypothesis was rejected, providing evidence for niche divergence (Table 2, Fig. 5).

Discussion

This study presents, to our knowledge, the first use of ENMs for lemurs in Madagascar that yield significant predictive ability based only on climatic variables (but see Kamilar & Muldoon, 2010 for some evidence of climatic niche differences in lemurs using Principal Component Analyses), adding further support to the hypothesis that climate has a large role in determining the distributions of species in Madagascar (e.g. Pearson & Raxworthy, 2009). Although our climate-based ENMs show overprediction in some areas in comparison with known ranges (e.g. our *E. collaris* ENM shows climatically suitable areas far to the north of their known range, which is likely restricted by the barrier of the Mananara River; Fig. 2), they show significant pre-

Table 2 Results of ENMTools analysis of niche equivalency (identity tests) and similarity (background tests) between sister taxa. See Figures 2–5 for histograms of the background tests.

Sister taxa	MD*	CD†	Niche Overlap *I*‡	Niche Overlap *D*§	Identity test *I*	Identity test *D*	Background test *I*	Background test *D*	Inference
E. collaris– E. cinereiceps	91.5	221.1	0.78	0.51	$P < 0.01$	$P < 0.01$	$P = 0.17, P = 0.90$	$P = 0.07, P = 0.92$	Null
E. rufus– E. rufifrons	72.9	506.6	0.28	0.08	$P < 0.01$	$P < 0.01$	$P = 0.04, P = 0.06$	$P = 0.78, P = 0.03$	Conservative/null
E. albifrons– E. sanfordi	126.7	303.4	0.36	0.14	$P < 0.01$	$P < 0.01$	$P = 0.44, P = 0.70$	$P = 0.45, P = 0.44$	Null
E. flavifrons–E. macaco	0.0	94.5	0.40	0.17	$P < 0.01$	$P < 0.01$	$P < 0.01, P = 0.02$	$P < 0.01, P = 0.04$	Divergent

*MD = Minimum geographic distance between occurrence records (km).
†CD = Geographic distance between the centroids of occurrence records (km).
‡I = Hellinger's I (Warren *et al.*, 2008).
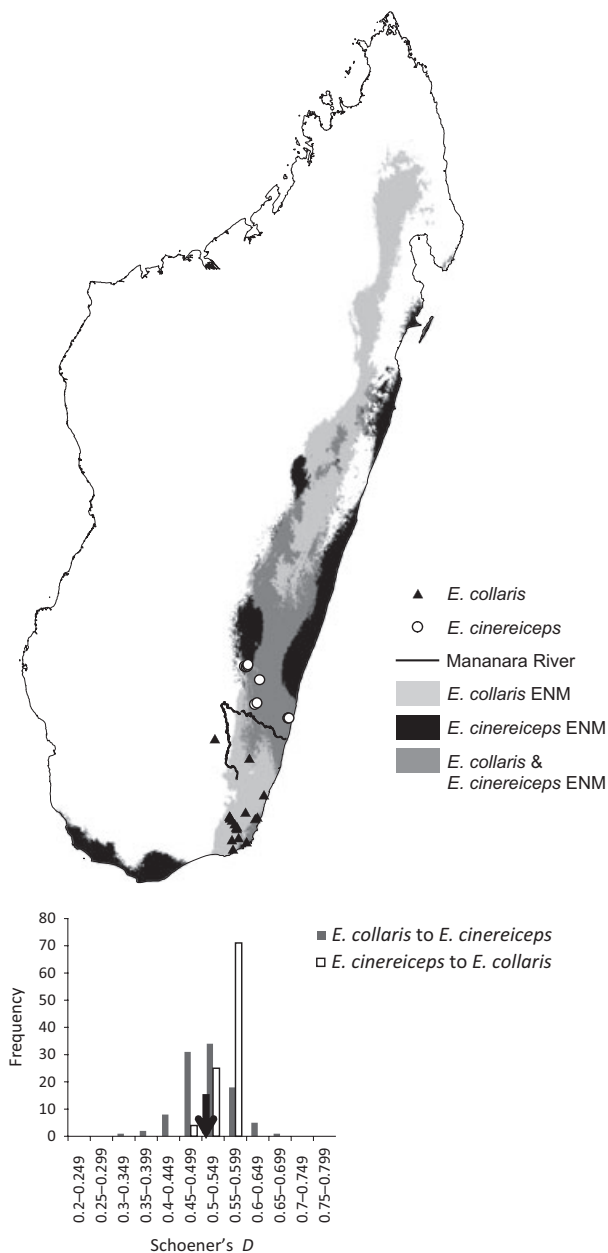§D = Schoener's D (Schoener, 1968).

Fig. 2 Geographic distribution of occurrence records, thresholded ecological niche models (ENMs) and histograms showing the results of the background test (Warren *et al.*, 2008) with 100 replicates for *E. collaris–E. cinereiceps*. The black arrow on the histograms shows where the actual species' ENM overlap falls compared to the null distribution of pseudo-replicated niche overlap values. The Mananara River is a putative allopatric barrier (see text).

Fig. 3 Geographic distribution of occurrence records, thresholded ecological niche models (ENMs) and histograms showing the results of the background test (Warren *et al.*, 2008) with 100 replicates for *E. rufus–E. rufifrons*. The black arrow on the histograms shows where the actual species' ENM overlap falls compared to the null distribution of pseudo-replicated niche overlap values. The Tsiribihina River is a putative allopatric barrier (see text).

dictive ability of occurrence records and in three cases successfully predict reported natural hybridization zones between taxa through spatial overlap of ENMs. This includes the Andringitra hybrid zone between the non-sister pair of *E. cinereiceps* and *E. rufifrons*, supported by
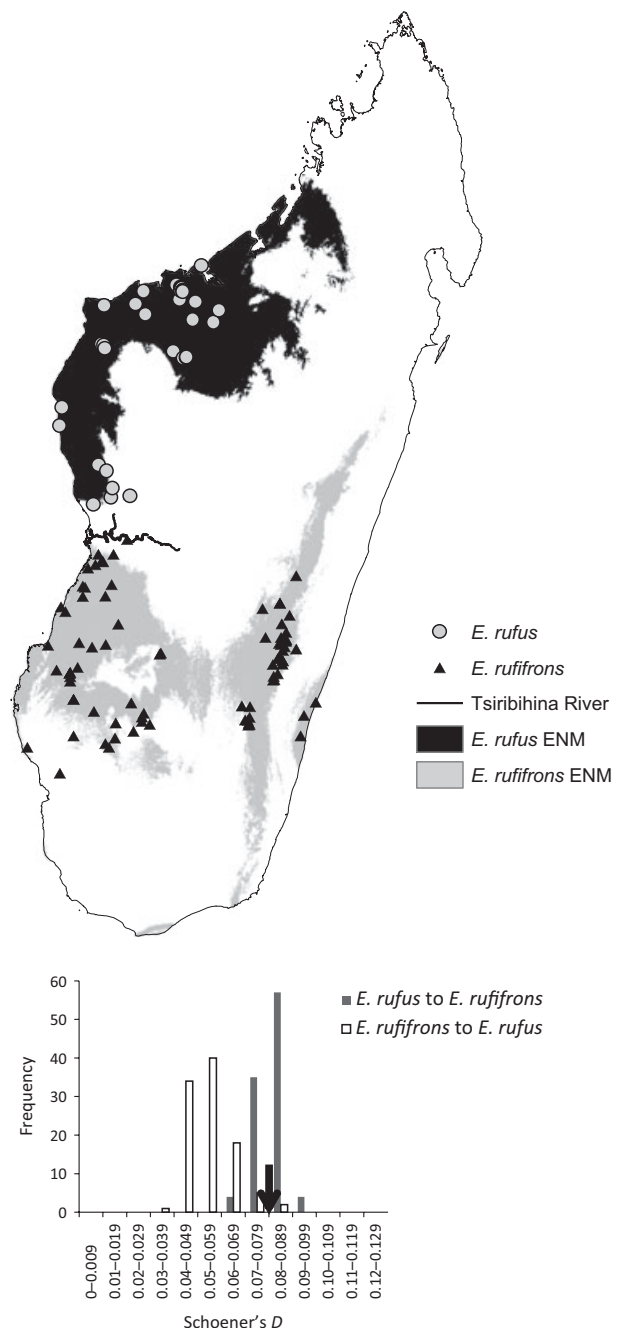
visual observations as well as genetic data (Sterling & Ramarason, 1996; Johnson & Wyner, 2000; Wyner *et al.*, 2002; Irwin *et al.*, 2005; Fig. 2,3) in addition to
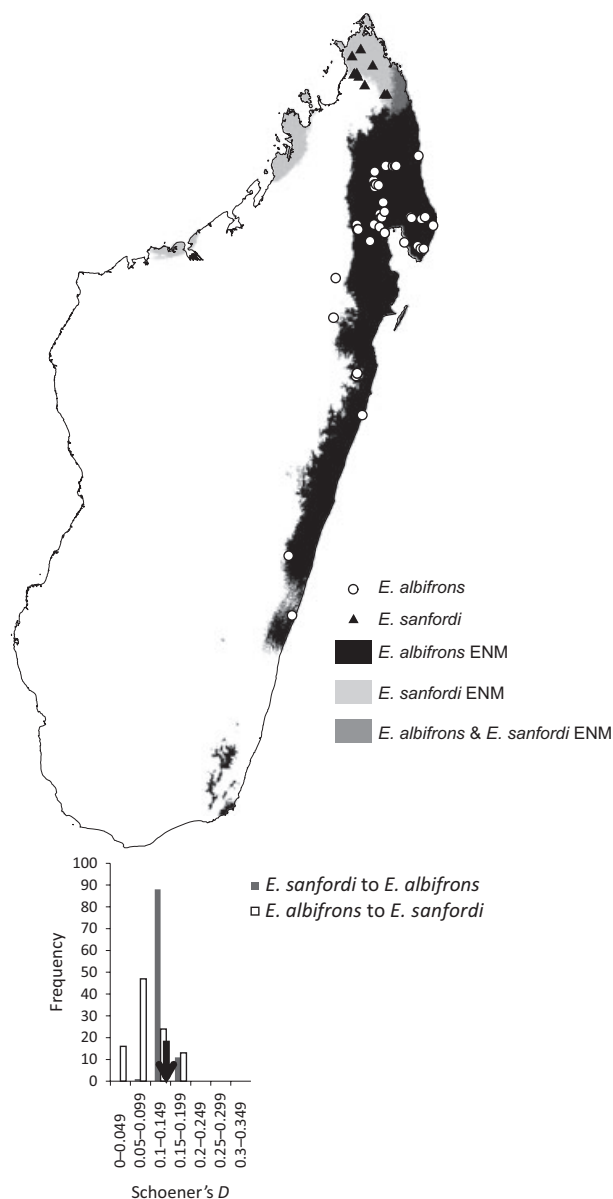
Fig. 4 Geographic distribution of occurrence records, thresholded ecological niche models (ENMs) and histograms showing the results of the background test (Warren *et al.*, 2008) with 100 replicates for *E. albifrons–E. sanfordi*. The black arrow on the histograms shows where the actual species' ENM overlap falls compared to the null distribution of pseudo-replicated niche overlap values.

the reported *E. albifrons–E. sanfordi* and *E. flavifrons–E. macaco* hybrid zones, which we discuss in more detail below.

We found nonequivalent niches between all pairs that we tested, suggesting a lack of ecological exchangeability between sister taxa. Following previous work that used differences in niches to support species delim-

itation (Wiens & Graham, 2005; Raxworthy *et al.*, 2007; Rissler & Apodaca, 2007), our results support the current species delimitation and in particular the recent elevation to species status of *E. flavifrons* and *E. macaco* (Mittermeier *et al.*, 2008). It is especially interesting that we found evidence for nonequivalent niches between *E. albifrons* and *E. sanfordi,* because the node for this pair has only been weakly supported by some genetic analyses (Wyner *et al.*, 1999; Pastorini *et al.*, 2003; Horvath *et al.*, 2008; Johnson *et al.*, 2008; Fig. S1). These taxa may be examples of 'cryptic' species lineages where morphological differences, lineage sorting and reproductive barriers may be incomplete, but ecological characters have differentiated (Avise, 2000; Futuyma, 2005; Raxworthy *et al.*, 2007). However, it has been noted recently (see Godsoe, 2010, 2012) that an inference of nonequivalency of ENMs, especially in allopatric species, may be largely the result of differential availability of habitat. The background test is meant to address this issue, and at least in the case of *E. flavifrons* and *E. macaco,* our interpretation of nonequivalent niches for this pair is consistent with our results from the background test (see further discussion below).

The sisters *E. collaris– E. cinereiceps* do not show either niche conservatism or divergence based on the background test, indicating that perhaps niche characteristics modelled here may not have been important for driving speciation. The climate within the selected background area for these species is quite similar despite *E. cinereiceps* having the most restricted range of any *Eulemur* species (between the Manampatrana and Mananara rivers), although precipitation values are slightly higher on average than those for *E. collaris* (precipitation in the driest quarter: mean, 191 mm; range, 73–314 mm for *E. cinereiceps*, mean, 143 mm; range, 46–394 mm for *E. collaris*). The climate similarity would explain the large amount of spatial overlap seen in their ENMs (Fig. 2). However, there is strong genetic and observational support for the Mananara River as a complete barrier between *E. cinereiceps* and *E. collaris* (Wyner *et al.*, 2002; Goodman & Ganzhorn, 2004). The null result from the background test combined with the barrier of the Mananara River thus best supports the allopatric speciation model for this sister pair. Although nonbiological reasons such as the resolution or selection of environmental predictors could have contributed to a lack of statistical power in this test, providing an alternative explanation as to why we could not reject the null hypothesis for this pair, the ENMs for these species showed strong predictive ability based on the included predictors. Furthermore, the presence of a clear allopatric barrier between the two species is in line with our hypotheses as laid out in the introduction.

Similarly, *E. rufus–E. rufifrons* have an allopatric distribution separated by the Tsiribihina River (Pastorini *et al.*, 2003), and our ENMs showed no spatial overlap
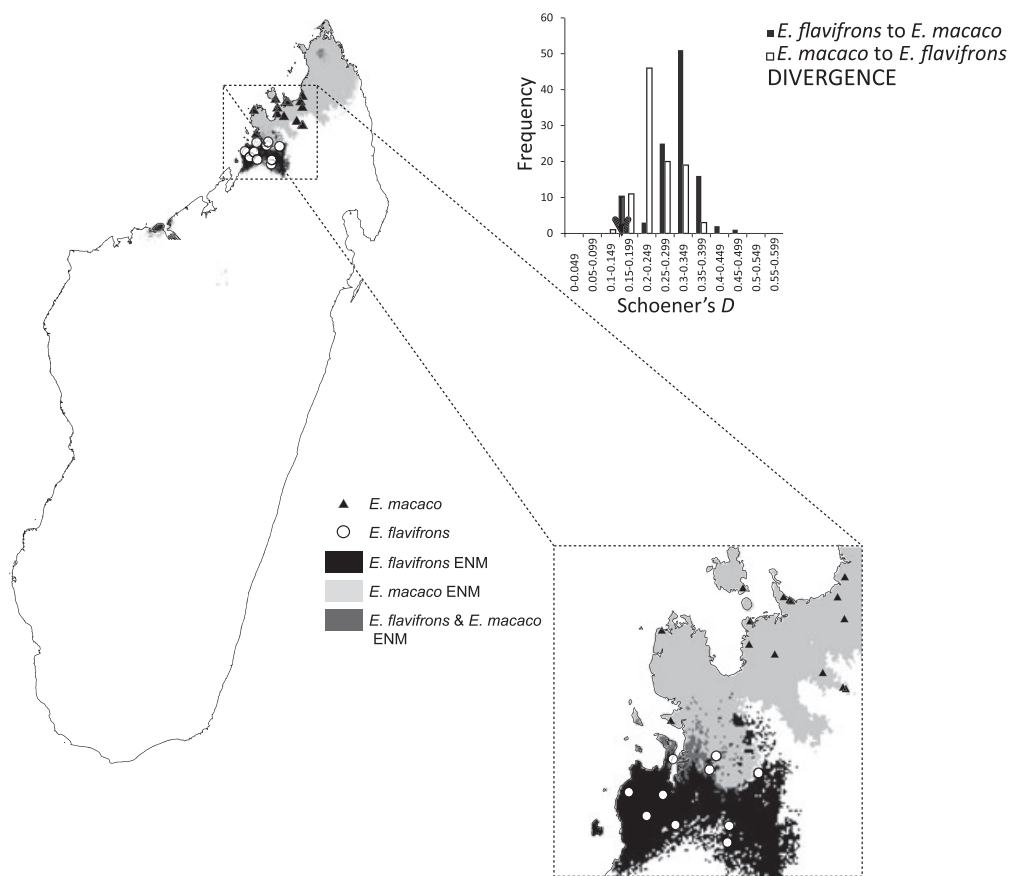
Fig. 5 Geographic distribution of occurrence records, thresholded ecological niche models (ENMs) and histograms showing the results of the background test (Warren *et al.*, 2008) with 100 replicates for *E. flavifrons–E. macaco*. The black arrow on the histograms shows where the actual species' ENM overlap falls compared to the null distribution of pseudo-replicated niche overlap values.

(Fig. 3) and very low niche overlap values (Table 2) between these taxa. However, despite very low overlap, our results from the background test showed weakly significant niche conservatism in one direction for both *I* and *D* (Table 2). Under a less-conservative interpretation of the background test, whereby significance in one direction and not the other is considered more than expected under the null hypothesis (Warren *et al.*, 2008; McCormack *et al.*, 2010), we would infer that *E. rufus–E. rufifrons* show evidence of niche conservatism. Because either interpretation would support our inference of the allopatric speciation model for this pair, we chose the more conservative approach in recognition of limitations of the background test. Specifically, the background test is sensitive to the heterogeneity of the environmental layers within the selected background area (Godsoe, 2010). For most of the species tested here, the species' range is well defined by a small area consisting of similar climate zones (*E. cinereiceps, E. collaris, E. flavifrons, E. macaco, E. rufus, E. sanfordi*); this is even true for *E. albifrons*,

which has a larger climatically suitable area (spatially) compared to other species, but remains restricted to moist forests that extend along the eastern escarpment within similar climate zones (Pearson & Raxworthy, 2009). However, *E. rufifrons* is an exception, extending from the west to the east coast and encompassing several disparate climate zones. Indeed, the range of precipitation values present within the selected background area of climate for *E. rufifrons* (precipitation of the coldest quarter 1–501 mm) is more than 35 times that for *E. rufus* (5–18 mm). Thus, despite *E. rufus– E. rufifrons* having the lowest niche overlap values of any pair studied, the background test produced a null distribution of very low overlap values as well, resulting in weakly significant evidence for niche conservatism in this pair. In recognition of the heterogeneous background area selected for *E. rufifrons* and its influence on the results of the background test, we took the conservative interpretation that we were unable to reject the null model, and find strongest support for allopatric speciation associated with a Tsiribihina River barrier.

We also did not reject the null hypothesis of the background test for *E. albifrons–E. sanfordi.* However, a distinct geographic barrier between these sister taxa is not clear. The Manambato River forms the southern limit for *E. sanfordi,* and the Bemarivo River forms the northern limit of *E. albifrons,* but these rivers are probably incomplete barriers as hybrids are also reported to occur between Vohemar and Sambava (Mittermeier *et al.,* 2006). Our ENMs also show spatial overlap in this region (Fig. 4). However, the climate zones occupied by these taxa are quite different, with *E. sanfordi* occupying dry deciduous and moist montane forests and *E. albifrons* moist lowland and montane rainforest. Precipitation in the driest quarter within the selected background area of climate for *E. albifrons* (mean 231 mm) is more than three times that of *E. sanfordi* (mean 63 mm). Population-level genetic data are needed to help clarify the status and extent of the putative hybrid zone, which may have formed as a result of secondary contact.

In contrast to the other three sister species pairs, for *E. flavifrons– E. macaco* we find strongest support for ecological parapatric speciation based on their significantly divergent niches (rejection of the null in the background test), relatively small centroid and minimum distances between occurrence points, and the lack of plausible geographic barriers on the occupied ecotone. The ENMs of these species were significantly less similar than would be expected based on the available habitat (Table 2, Fig. 5), suggesting that ecological divergence has played a role in speciation. This is further supported by the lack of geographic barriers between these sister species – the Andranomalaza River does not form a complete barrier, with *E. flavifrons* occurring north-east of the River, just to the east of the Manongarivo Special Reserve (Andrianjakarivelo, 2004). There is also a possible hybrid zone (based on reported observations of intermediate morphology forms) north of the Andranomalaza River in the Manongarivo Massif region, between Maromandia and Ambanja (Meyers *et al.,* 1989; Rabarivola *et al.,* 1991; Andrianjakarivelo, 2004; Schwitzer *et al.,* 2005, 2006), but this has not yet been confirmed by genetic studies. This suspected hybridization zone occurs in the area of spatial overlap between ENMs for *E. flavifrons–E. macaco* (Fig. 5).

An environmental gradient is present between the ranges of *E. macaco* and *E. flavifrons*, with *E. macaco* inhabiting tropical moist lowland and montane forest and *E. flavifrons* inhabiting subtropical moist and dry forests in the transition zone between the Sambirano region to the north and the western dry deciduous forests to the south. Although temperature values are similar within the selected background area of climate for both species (minimum temperature of the coldest month: mean, 17 °C; range, 8–20 °C for *E. macaco,* mean, 18 °C; range, 11–19 °C for *E. flavifrons*;

temperature annual range: mean, 15 °C; range, 12–18 °C for *E. macaco,* mean, 15 °C; range, 14–17 °C for *E. flavifrons*), precipitation values are very different. Precipitation of the driest and coldest quarters within *E. flavifrons'* range (for both driest and coldest: mean, 25 mm; range, 14–40 mm) is less than half that of *E. macaco*'s (driest: mean, 57 mm; range, 26–103 mm; coldest: mean, 58 mm; range, 26–103 mm). We conjecture that transitional environments such as the Sambirano–dry forest transition zone may present environmental gradients that offer a higher likelihood for parapatric speciation processes, although additional comparisons across several taxonomic groups would be necessary to test this idea. Several other studies have found evidence that ecological divergence may play an important role in the diversification process of a clade, although typically from ectothermic vertebrates (e.g. in Dendrobatid frogs, Graham *et al.,* 2004; *Phelsuma* day geckos, Raxworthy *et al.,* 2007; *Sistrurus* rattlesnakes, Wooten & Gibbs, 2012). It is therefore of particular interest that we find evidence of niche divergence for a mammal. A next step to explore ecological divergence between *E. flavifrons–E. macaco* would be to collect higher-resolution genetic data at the population level, to test whether genetic distances correlate with ecological distances (Kozak & Wiens, 2006).

Our results are consistent with parapatric speciation along an ecotone, but are not only the possible explanation for divergent ecological niches between sister species. For example, post-speciation ecological divergence could also explain our results (Losos & Glor, 2003; Graham *et al.,* 2004; Swenson, 2008) if we assume there was range expansion from unknown allopatric areas (that do not fit obvious landscape features), with allopatric ecological niche divergence or character displacement of niches in secondary contact zones. The methods we used here may not be able to distinguish between parapatric speciation and post-speciation divergence as the explanation for our results, as either process would cause divergent niches in species that are geographically close to one another. However, niche divergence is an important piece of evidence that can inform our inference of speciation process, especially when combined with other factors including the presence or absence of certain geographic and environmental features. We contend that the accumulation of evidence presented here most strongly supports parapatric speciation via ecological divergence between *E. flavifrons– E. macaco.* Also consistent with this explanation, *E. flavifrons* and *E. macaco* have diagnostic pelage and eye colour characteristics that might facilitate assortative mating, a critical component for parapatric speciation (Fisher, 1958). *Eulemur macaco* has brown or red eyes, prominent ear tufts and darker coloured females, whereas *E. flavifrons* has blue or grey eyes, no ear tufts and lighter coloured females (male pelage in both species is black; Meyers *et al.,* 1989).

Overall, we thus find support for multiple divergence processes among lemurs in Madagascar. These findings agree with other studies that have reported multiple speciation mechanisms within closely related taxonomic groups (e.g. in North American salamanders, Kozak & Wiens, 2006; North American grasshoppers, Carstens & Knowles, 2007; common kingsnakes, Pyron & Burbrink, 2009), which more generally suggests that landscapes can facilitate speciation through both population isolation and ecotone adaptation. In addition, our results support conserving intact ecotones as a means to maintain evolutionary processes, as well as demonstrate the utility of using ecological divergence to help recognize cryptic species.

Acknowledgments

References

Anderson, R.P., Gomez-Laverde, M. & Peterson, A.T. 2002. Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecol. Biogeogr.* **11**: 131–141.

Andrianjakarivelo, V. 2004. *Exploration de la zone en dehors de la peninsule Sahamalaza pour l'évaluation rapide de la population d'E. m. flavifrons. Report*. Wildlife Conservation Society, Antananarivo, Madagascar.

Avise, J. 2000. *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, MA.

Carstens, B. & Knowles, L. 2007. Shifting distribution and speciation: species divergence during rapid climate change. *Mol. Ecol.* **16**: 619–627.

Dewar, R.E. & Richard, A.F. 2007. Evolution in the hypervariable environment of Madagascar. *Proc. Natl. Acad. Sci. USA* **104**: 13723–13727.

Elith, J., Graham, C. & NCEAS. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**: 129–151.

Fielding, A.H. & Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**: 38–49.

Fisher, R. 1958. *The Genetical Theory of Natural Selection*, 2nd edn. Dover, New York.

Franklin, J. 2009. *Mapping Species Distributions*. Cambridge University Press, Cambridge.

Futuyma, D. 2005. *Evolution*. Sinauer, Sunderland, MA.

Ganzhorn, J.U. & Randriamanalina, M. 2004. Les lemuriens de la foret de Mikea. In: *Inventaire floristique et faunistique de la foret de Mikea*, vol. **21** (A. Raselimanana, S.M. Goodman, eds), pp. 87–93. Ministere de l'Education Nationale et de la Recherche Scientifique, Antananarivo.

Ganzhorn, J.U., Goodman, S.M., Nash, S.D. & Thalmann, U. 2006. Lemur biogeography. In: *Primate Biogeography: Progress and Prospects* (S. Lehman, J. Fleagle, eds), pp. 229–254. Springer, New York.

Gasse, F. & Van Campo, E. 1998. A 40 000-yr pollen and diatom record from Lake Tritrivakely, Madagascar, in the southern tropics. *Quaternary Res.* **49**: 299–311.

Gasse, F. & Van Campo, E. 2001. Late Quaternary environmental changes from a pollen and diatom record in the southern tropics (Lake Tritrivakely, Madagascar). *AAPG Stud. Geol.* **167**: 287–308.

Godsoe, W. 2010. Regional variation exaggerates ecological divergence in niche models. *Syst. Biol.* **59**: 298–306.

Godsoe, W. 2012. Are comparisons of species distribution models biased? Are they biologically meaningful? *Ecography* **35**: 769–779.

Goodman, S.M. & Ganzhorn, J.U. 2004. Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *J. Biogeogr.* **31**: 47–55.

Goodman, S.M., Razafindratsita, V., Schutz, H. & Ratsimbazafy, R. 2001. Chapitre 10. Les lémuriens. In: *Inventaire biologique du Parc National de Ranomafana et du couloir forestier qui la relie au Parc National d'Andringitra*, Vol. Recherches pour le developpement. Serie Sciences biologiques No. 17 (S.M. Goodman & V. Razafindratsita, eds), pp. 231–243. Centre d'information et de documentation scientifique et technique, Antananarivo, Madagascar.

Graham, C., Ron, S., Santos, J., Schneider, C. & Moritz, C. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in Dendrobatid frogs. *Evolution* **58**: 1781–1793.

Groves, C. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.

Groves, C. 2006. Red-fronted lemurs are not the same as red lemurs. Paper presented at 24th annual conference of Australasian primate society, Perth, 1-2 April. *Aus. Primatol.* **18**: 23.

Gudde, R., Joy, J. & Mooers, A. 2013. Imperiled phylogenetic endemism of Malagasy lemuriformes. *Divers. Distrib.* **19**: 664–675.

Hickerson, M., Carstens, B., Cavender-Bares, J., Crandall, K.A., Graham, C., Johnson, J. *et al.* 2010. Phylogeography's past, present, and future: 10 years after Avise, 2000. *Mol. Phylo. Evol.* **54**: 291–301.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**: 1965–1978.

Horvath, J.E., Weisrock, D.W., Embry, S.L., Fiorentino, I., Balhoff, J.P., Kappeler, P. *et al.* 2008. Development and application of a phylogenomic toolkit: resolving the evolutionary history of Madagascar's lemurs. *Genome Res.* **18**: 489–499.

Irwin, M.T., Johnson, S. & Wright, P.C. 2005. The state of lemur conservation in southeastern Madagascar: population assessments for diurnal lemurs using surveys, satellite imagery and GIS. *Oryx* **39**: 1–15.

IUCN. 2012. IUCN red list of threatened species. Version 2012.1. URL www.iucnredlist.org.

Johnson, S.E. & Wyner, Y. 2000. Notes on the biogeography of *E. f. albocollaris*. *Lemur News* **5**: 25–28.

Johnson, S.E., Lei, R., Martin, S.K., Irwin, M.T. & Louis, E.E. Jr 2008. Does *Eulemur cinereiceps* exist? preliminary evidence from genetics and ground surveys in Southeastern Madagascar. *Am. J. Primatol.* **70**: 372–385.

Kamilar, J. & Muldoon, K. 2010. The climatic niche diversity of Malagasy primates: a phylogenetic perspective. *PLoS ONE* **5**: e11073.

Kozak, K. & Wiens, J. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* **60**: 2604–2621.

Lawler, R.R., Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. & Caswell, H. 2009. Demography of a wild lemur population in a stochastic rainfall environment. *Oecologia* **161**: 491–504.

Linnaeus, C. 1766. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differntiis, Dynonymis, Locis*, 12th edn. Laurentius Salvius, Stockholm.

Losos, J. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11**: 995–1003.

Losos, J. & Glor, R. 2003. Phylogenetic comparative methods and the geography of speciation. *Trends Ecol. Evol.* **18**: 220–227.

MacColl, A. 2011. The ecological causes of evolution. *Trends Ecol. Evol.* **26**: 514–522.

Maeve, J. & Kellman, M. 1994. Maintenance of rain forest diversity in riparian forests of tropical savannas: implications for species conservation during Pleistocene drought. *J. Biogeogr.* **21**: 121–135.

Martin, R.D. 1972. Adaptive radiation and behaviour of the Malagasy lemurs. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **264**: 295–352.

Martin, R.D. 1995. Prosimians: from obscurity to extinction? In: *Creatures of the Dark* (L. Alterman, K. Izard, G. Doyle, eds), pp. 535–563. Plenum, New York.

McCormack, J.E., Zellmer, A.J. & Knowles, L. 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? Insights from tests with niche models. *Evolution* **64**: 1231–1244.

Meyers, D., Rabarivola, C. & Rumpler, Y. 1989. Distribution and conservation of Sclater's lemur: implications of a morphological cline. *Prim. Conserv.* **10**: 77–81.

Mittermeier, R.A., Konstant, W.R., Hawkins, F., Louis, E.E. Jr, Langrand, O., Ratsimbazafy, J. *et al.* 2006. *Lemurs of Madagascar*, 2nd edn. Conservation International, Washington, D.C.

Mittermeier, R.A., Ganzhorn, J.U., Konstant, W.R., Glander, K., Tattersall, I., Groves, C.P. *et al.* 2008. Lemur diversity in Madagascar. *Int. J. Primatol.* **29**: 1607–1656.

Moritz, C., Patton, J., Schneider, C. & Smith, T. 2000. Diversification of rainforest faunas: an integrated molecular approach. *Annu. Rev. Ecol. Syst.* **31**: 533–563.

Pastorini, J., Thalmann, U. & Martin, R.D. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proc. Natl. Acad. Sci. USA* **100**: 5879–5884.

Pastorini, J., Zaramody, A., Curtis, D.J., Nievergelt, C. & Mundy, N. 2009. Genetic analysis of hybridization and introgression between wild mongoose and brown lemurs. *BMC Evol. Biol.* **9**: 32.

Pearce, J. & Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Modell.* **133**: 225–245.

Pearson, R.G. & Raxworthy, C.J. 2009. The evolution of local endemism in Madagascar: watershed versus climatic gradient hypotheses evaluated by null biogeographic models. *Evolution* **63–4**: 959–967.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* **34**: 102–117.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M. *et al.* 2011. *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton, NJ.

Phillips, S.J. & Dudik, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.

Phillips, S.J., Dudik, M. & Schapire, R.E. 2004. A maximum entropy approach to species distribution modeling. *Proceedings of the Twenty-First International Conference on Machine Learning*, pp. 655–662. Association for Computer Machinery Press, Banff, Canada.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**: 231–259.

Pyron, R.A. & Burbrink, F.T. 2009. Lineage diversification in a widespread species: roles for niche divergence and conservatism in the common kingsnake, *Lampropeltis getula*. *Mol. Ecol.* **18**: 3443–3457.

Rabarivola, C., Meyers, D. & Rumpler, Y. 1991. Distribution and morphological characters of intermediate forms between the black lemur (*Eulemur macaco macaco*) and the Sclater's lemur (*E. m. flavifrons*). *Primates* **32**: 269–273.

Raxworthy, C.J., Ingram, C., Rabibisoa, N. & Pearson, R.G. 2007. Applications of Ecological Niche Modeling for Species Delimitation: a Review and Empirical Evaluation Using Day Geckos (*Phelsuma*) from Madagascar. *Syst. Biol.* **56**: 907–923.

Richard, A.F., Dewar, R.E., Schwartz, M. & Ratsirarson, J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *J. Hum. Evol.* **39**: 381–391.

Rissler, L. & Apodaca, J. 2007. Adding more ecology into species delimitation: ecological niche modeling and phylogeography help define cryptic species in the Black Salamander (*Aneides flavipunctatus*). *Syst. Biol.* **56**: 924–942.

Roos, C., Zinner, D., Kubatko, L.S., Schwarz, C., Yang, M., Meyers, D. *et al.* 2011. Nuclear versus mitochondrial DNA: evidence for hybridization in colobine monkeys. *BMC Evol. Biol.* **11**: 77.

Schneider, C., Smith, T., Larison, B. & Mortiz, C. 1999. A test of alternative models of diversification in tropical rainforests: Ecological gradients vs. rainforest refugia. *Proc. Natl. Acad. Sci. USA* **96**: 13869–13873.

Schoener, T. 1968. Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704–726.

Schwitzer, C., Schwitzer, N., Randriatahina, G.H. & Kaumanns, W. 2005. Inventory of the *Eulemur macaco flavifrons* population in the Sahamalaza protected area, Northwestern Madagascar, with notes on an unusual color variant of *E. macaco*. *Göttinger Freilandtage 'Primate Diversity - Past, Present and Future' Prim R. SI* **72–1**: 39–40.

Schwitzer, C., Schwitzer, N., Randriatahina, G.H., Rabarivola, C., Kaumanns, W. 2006. "Programme Sahamalaza": new perspectives for the *in situ* and ex situ study and conservation of the blue-eyed black lemur (*Eulemur macaco flavifrons*) in a fragmented habitat. In: *Proceedings of the German-Malagasy research cooperation in life and earth sciences*

(C. Schwitzer, S. Brandt, O. Ramilijaona, M. Rakotomalala, D. Ackermand, T. Razakamanana & J. Ganzhorn, eds), pp. 135–149. Concept Verlag, Berlin.

Simons, E. & Rumpler, Y. 1988. *Eulemur*. New generic name for species of *Lemur* other than *Lemur catta*. *Comptes Rendus de l'Academie des Science Serie III. Sciences de la Vie-Life Sciences* **307**: 547–551.

Smith, T., Wayne, R., Girman, D. & Bruford, M. 1997. A role for ecotones in generating rainforest biodiversity. *Science* **276**: 1855–1857.

Sterling, E. & Ramarason, M. 1996. Rapid assessment of the primate fauna of the eastern slop of the Reserve Naturelle Integrale d'Andringitra, Madagascar. *Fieldiana: Zoology* **85**: 293–305.

Swenson, N. 2008. The past and future influence of geographic information systems on hybrid zone, phylogeographic and speciation research. *J. Evol. Biol.* **21**: 421–434.

Tattersall, I. 1982. *The Primates of Madagascar*. Columbia University Press, New York.

Warren, D., Glor, R. & Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**: 2868–2883.

Warren, D., Glor, R. & Turelli, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33**: 607–611.

Wiens, J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* **58**: 193–197.

Wiens, J. & Graham, C. 2005. Niche Conservatism: integrating Evolution, Ecology, and Conservation Biology. *Ann. Rev. Ecol. Syst.* **36**: 519–539.

Wiens, J., Ackerly, D., Allen, A., Anacker, B., Buckley, L., Cornell, H. *et al.* 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**: 1310–1324.

Wilmé, L., Goodman, S.M. & Ganzhorn, J.U. 2006. Biogeographic evolution of Madagascar's microendemic biota. *Science* **312**: 1063–1065.

Wooten, J.A. & Gibbs, H.L. 2012. Niche divergence and lineage diversification among closely related *Sistrurus* rattlesnakes. *J. Evol. Biol.* **25**: 317–328.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: coping with an Island environment. *Yearb. Phys. Anthropol.* **42**: 31–72.

Wyner, Y., Absher, R., Amato, G., Sterling, E., Stumpf, R., Rumpler, Y. *et al.* 1999. Species concepts and the determination of historic gene flow patterns in the *Eulemur fulvus* (Brown Lemur) complex. *Biol. J. Linn. Soc.* **66**: 39–56.

Wyner, Y., Johnson, S.E., Stumpf, R. & DeSalle, R. 2002. Genetic assessment of a white-collared X red-fronted lemur hybrid zone at Andringitra, Madagascar. *Am. J. Primatol.* **57**: 51–66.

Yoder, A.D. & Irwin, J.A. 1999. Phylogeny of the Lemuridae: effects of character and taxon sampling on resolution of species relationships with in *Eulemur*. *Cladistics* **15**: 351–361.

Zinner, D., Arnold, M.L. & Roos, C. 2011. The strange blood: natural hybridization in primates. *Evol. Anthropol.* **20**: 96–103.

Supporting information

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

Table S1 Summary of taxonomic assessments of the genus *Eulemur*.

Table S2 Occurrence points used to build *Eulemur* sister species ecological niche models, modified from Wilmé *et al.* (2006).

Figure S1 Molecular-based phylogenetic trees representing the results of (a) Horvath *et al.* (2008) approximately 16 000 bp nuclear and mtDNA, (b) Wyner *et al.* (1999) approximately 1250 bp mtDNA, (c) Pastorini *et al.* (2003) approximately 2400 bp mtDNA, (d) Johnson *et al.* (2008) approximately 2950 bp mtDNA, and (e) Gudde *et al.* (2013) approximately 13 000 bp nuclear and mtDNA.