

Ecological niche modeling of mouse lemurs (*Microcebus* spp.) and its implications for their species diversity and biogeography

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Introduction

Recent studies of lemur species diversity have particularly focused on mouse lemurs (Cheirogaleidae: *Microcebus*) – small, nocturnal, and superficially monotypic creatures (Radespiel *et al.*, 2012; Zimmermann and Radespiel, 2014). *Microcebus* is widespread across the diverse habitats of Madagascar, and are present in primary, secondary, and disturbed forest types where suitable area remains (Mittermeier *et al.*, 2010). Until the end of the last century, it was assumed that diversity in mouse lemurs consisted only of two morphologically and geographically distinct species – a larger, grayish western morph, *Microcebus murinus*, and a smaller, reddish eastern species, *M. rufus* (Mittermeier *et al.*, 1994). Each of these species was thought to have broad distribution, encompassing a relatively diverse array of climates and habitats. In addition, mouse

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lemurs were believed to have largely allopatric distributions, with very little, if any, sympatry observed. However, the number of recognized mouse lemur species on Madagascar has vastly increased in recent years with an emphasis on methods to delineate cryptic species in the field (Mittermeier *et al.*, 2010). There are currently 21 formally described species of mouse lemur, including some taxa that have sympatric distributions (Zimmermann and Radespiel, 2014).

Some controversy exists over the taxonomic validity over the newly named species, associated in large part with problems of sample size and geographic coverage, and difficulty in distinguishing clinal variation from distinct phylogenetic species (Tattersall, 2007; Markolf *et al.*, 2011). Although cryptic species are often differentiated solely on the basis of genetics (Pastorini *et al.*, 2001; Olivieri *et al.*, 2007; Horvath *et al.*, 2008; Groeneveld *et al.*, 2009; Weisrock *et al.*, 2012), integrative studies of primate taxonomy have recently used diet, social system, communication signals, sleeping site ecology, and reproductive behavior to delineate species boundaries (Kamilar, 2006; Radespiel *et al.*, 2006; Zimmermann, 2013; Zimmermann and Radespiel, 2014). Such studies have demonstrated that sympatric species of *Microcebus* coexist in several regions of Madagascar (Yoder *et al.*, 2005; Weisrock *et al.*, 2010; Rasoloarison *et al.*, 2013). Thus, mouse lemurs provide an excellent opportunity to investigate the evolutionary and ecological mechanisms that allow species to coexist.

One relatively new tool to investigate species diversity and species delineation is ecological niche modeling (i.e., species distribution modeling; Elith *et al.*, 2006; Phillips *et al.*, 2006). Ecological niche models can be applied to questions of species delineation because this method can provide new information regarding the distribution and ecological niche separation across a set of taxa. Raxworthy *et al.* (2007) used this

approach to investigate the biogeography and taxonomy of Malagasy day geckos (genus *Phelsuma*). Although the taxa exhibited some degree of genetic and morphological disparity, ecological niche models performed significantly better when taxa were divided into separate species, rather than subspecies. These findings supported the elevation of three species to full species status, as well as a new species being named. A recent paper by Blair *et al.* (2013) used ecological niche models to explicitly test whether closely related *Eulemur* taxa exhibited significantly divergent niche spaces. They found that some sister species displayed niches no different than expected by chance, implying an allopatric mode of speciation because a failure to adapt to new environments might be hypothesized when populations are spatially isolated from each other. In other words, spatial isolation may be facilitated by ecological niche conservatism (Wiens, 2004). In contrast, one pair of species displayed significantly different ecological niches, suggesting a parapatric model of speciation.

While it is not our intent to evaluate the validity of newly named species of *Microcebus*, an analysis of ecological niche space can be useful for testing hypotheses about species diversity in mouse lemurs, and evaluating species divergence between sympatric sister species. 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). Studies of the degree to which ecological niches vary across a phylogeny are crucial for understanding how and when environmental factors can influence natural selection and generate biological diversity (Wiens, 2004; Kamilar and Muldoon, 2010; Wiens *et al.*, 2010; MacColl, 2011; Kamilar and Cooper, 2013). The goal of our chapter is thus to evaluate the species diversity of mouse lemurs by using an ecological niche modeling approach. Specifically, we

quantified mouse lemur climatic niches and tested the degree of niche overlap among species. Generating niche models can inform us about the potential distribution of taxa, and consequently the possibility of species co-occurrence. In addition, niche models with good predictive power indicate that a species distribution is strongly related to climatic factors. In contrast, species with poorly performing models may indicate that they are ecological generalists and not well connected to climatic factors and/or that multiple species may actually exist. Finally, examining the degree of niche overlap among taxa, especially sister species, can provide insights into speciation mechanisms.

In this chapter, we have the following goals: (1) generate ENMs for six mouse lemur species to determine how well climatic variable predict their distributions, (2) examine the degree of niche overlap among these species and discuss these results in the context of their geographic distribution and taxonomy. Ideally, we would have examined the ecological niche space of all mouse lemur species, though the available data limited us to examining six species, two of which are sister species (*M. griseorufus* and *M. murinus*) according to the phylogeny presented in several recent sources (Springer *et al.*, 2012; Weisrock *et al.*, 2012; Thiele *et al.*, 2013).

Methods

Data collection

We used known locality data from unpublished as well as published sources (Kamilar and Muldoon, 2010). The data from Kamilar and Muldoon (2010) were originally sourced from Wilmé *et al.* (2006) and supplemented with published and unpublished data provided by KMM, Shawn Lehman, and other field researchers (e.g. Muldoon and

Goodman, 2010). Our analyses required a minimum of 10 known localities per species. Based on this criterion and the available data, we included six mouse lemur species in our study: *Microcebus griseorufus*, *M. murinus*, *M. myoxinus*, *M. ravelobensis*, *M. rufus*, and *M. tavaratra*. We used a total of 125 localities, with the number of localities per species presented in Table 23.1 and visually displayed in Figure 23.1.

Table 23.1.

Maxent results using climatic variables to model the distribution of mouse lemur species.

| Species | N* | Mean test AUC | Test AUC SD | Omission error –fold 1** | Omission error –fold 2** | Omission error –fold 3** | Omission error –fold 4** |
|--------------------------------|----|---------------|-------------|--------------------------|--------------------------|--------------------------|--------------------------|
| <i>Microcebus griseorufus</i> | 32 | 0.926 | 0.018 | 0, $P < 0.001$ | 0, $P < 0.001$ | 0.125, $P < 0.001$ | 0, $P < 0.001$ |
| <i>Microcebus murinus</i> | 34 | 0.680 | 0.123 | 0.111, $P = 0.521$ | 0, $P = 0.056$ | 0, $P = 0.103$ | 0.125, $P = 0.568$ |
| <i>Microcebus myoxinus</i> | 12 | 0.890 | 0.021 | 0, $P = 0.008$ | 0, $P = 0.008$ | 0, $P = 0.008$ | 0.333, $P = 0.101$ |
| <i>Microcebus ravelobensis</i> | 10 | 0.987 | 0.007 | 0, $P < 0.001$ | 0, $P < 0.001$ | 0, $P = 0.002$ | 0.5, $P = 0.032$ |
| <i>Microcebus rufus</i> | 23 | 0.919 | 0.027 | 0.167, $P = 0.001$ | 0.167, $P = 0.004$ | 0, $P = 0.004$ | 0, $P = 0.001$ |
| <i>Microcebus tavaratra</i> | 14 | 0.980 | 0.003 | 0, $P < 0.001$ | 0.500, $P = 0.003$ | 0, $P < 0.001$ | 0, $P < 0.001$ |

*Number of localities used to build model. **Under a minimum training presence threshold.

Our ecological niche models were defined by six climate variables that characterized various aspects of rainfall and temperature: (1) isothermality, (2) temperature seasonality, (3) minimum temperature of coldest month, (4) temperature annual range, (5) precipitation of driest quarter, and (6) precipitation of coldest quarter. These and similar climatic variables are good proxies for the various habitat types that exist in Madagascar (Kamilar and Muldoon, 2010) and are likely related to lemur physiology and life history (Wright, 1999; Dewar and Richard, 2007). In addition, these measures of climatic variation were recently used in a niche modeling study of

Eulemur species (Blair *et al.*, 2013). All climate data were obtained from the Worldclim database (Hijmans *et al.*, 2005), with an approximate 1 km resolution.

Figure 23.1

Species localities included in our analyses.

Data analysis

We used Maxent (version 3.3.3k; Phillips *et al.*, 2006; Phillips and Dudík, 2008) to construct climate-based distribution models for each species. Maxent employs a machine learning algorithm to predict the distribution of species using known occurrences. In the past five years, Maxent has become the most commonly used method to construct species distribution models. Previous research evaluating a variety of niche modeling methods found that Maxent performs as well or better than other software packages (Elith *et al.*, 2006). In addition, one advantage of Maxent is that it only requires known presence data (as opposed to known absences as well). This is particularly advantageous for our study because mouse lemurs are cryptic animals. Their nocturnal lifestyle, small body size, and relatively dispersed social structure (Zohdy *et al.*, 2012) make it difficult to be certain that species are absent from a particular location.

For each species, we used 75% of their known localities as training data and set the remaining localities as test data. We used a regularization multiplier equal to one for all species. As lower values may yield overfitted models (Radosavljevic and Anderson, 2013), we also examined models using regularization multipliers equal to two and three. Yet, using these latter regularization multipliers produced models that were similar or performed less well. One way we judged model performance is based on area under the curve (AUC) values of the receiver operating curve plots. An AUC value of 0.5

indicates that the model is no better than random at predicting the presence of a species at a locale. An AUC values greater than 0.5 suggests improved model performance, with values of 1.0 indicating a model with perfect predictive ability. However, AUC values are known to be influenced by the total niche space occupied by a species. Taxa occupying narrow environmental niches (relative to the total available niche space) tend to have higher AUC values compared to other species. In addition, we followed the default recommendations from the Maxent developers for the other model options (Phillips *et al.*, 2006; Phillips and Dudík, 2008).

As recommended and performed by recent studies (Peterson *et al.*, 2011; Blair *et al.*, 2013), we implemented a fourfold cross-validation procedure that randomly splits the occurrence data into equal sized groups. This approach is advantageous because it uses all data for validation, which is especially useful for small data sets. This is important considering the relatively small sample size for most of our species. Using fourfold partitioning yields four models per species, with AUC values produced for each model. We present the mean test AUC for each species, as well as the standard deviation for the models. In addition, we used a binomial test of omission to calculate the statistical significance of each model's prediction (Anderson *et al.*, 2002). We present the detailed results produced by each model for each species.

We calculated the niche overlap based on the distribution models for all pairwise-species using Schoener's D (Schoener, 1968) and Hellinger's I (Warren *et al.*, 2008). Both metrics vary from zero to one, indicating no niche overlap to complete niche overlap, respectively. These values were quantified using the ENMtools software (Warren *et al.*, 2010). In addition, we tested whether species exhibited significantly different niches using the identity test feature in ENMtools. This procedure pools all the

locality data for each species-pair and then randomly assigns localities to two new “pseudo” species. We repeated this procedure 100 times to create a distribution of random species-pairs with associated niche overlap values, and then compared the niche overlap of the real species-pair to this hypothetical distribution. We considered the ecological niches of species-pairs to be significantly different if their overlap value was lower than the five lowest values from the randomized distribution. This is equivalent to a one-tailed test with an accepted alpha level of 0.05.

Results

Maxent predictive models performed well for five of the six mouse lemur species examined, with the exception being *Microcebus murinus* (Table 23.1 and Figure 23.2A–E). For the five species that exhibited niche models that were well predicted, their mean test AUC values ranged from 0.890 to 0.987. Four of these five species exhibited statistically significant binomial tests for all of the four folds (p values ranged from < 0.001 to 0.032 and most omission errors were 0, and ranged from 0 to 0.5). The remaining species, *M. myoxinus*, exhibited a significant binomial test for three of four folds ($p = 0.008$ – 0.101 and omission errors from 0 to 0.333). For *M. murinus*, omission errors ranged from 0 to 0.125 and p values ranged from 0.056 to 0.568.

The niche overlap values for species-pairs ranged from 0.022 (*M. rufus*–*M. ravelobensis*) to 0.779 (*M. murinus*–*M. griseorufus*) for Hellinger’s I and 0.002 (*M. rufus*–*M. ravelobensis*) to 0.554 (*M. myoxinus*–*M. murinus*) for Schoener’s D (Tables 23.2 and 23.3). We found significantly low overlap values for all pairwise comparisons and for both overlap indices. In fact, the lowest possible p value was found in all cases

($p < 0.01$). *M. murinus* exhibited the highest niche overlap values on average, which is in accordance with their broadly predicted niche distribution (Figure 23.2B).

Table 23.2.

Niche overlap results using Hellinger's I. Higher I values indicate greater niche overlap between species.

| Species | <i>M. griseorufus</i> | <i>M. murinus</i> | <i>M. myoxinus</i> | <i>M. ravelobensis</i> | <i>M. rufus</i> | <i>M. tavaratra</i> |
|--------------------------------|-----------------------|-------------------|--------------------|------------------------|-----------------|---------------------|
| <i>Microcebus griseorufus</i> | × | 0.779 | 0.471 | 0.171 | 0.499 | 0.174 |
| <i>Microcebus murinus</i> | < 0.01 | × | 0.778 | 0.502 | 0.593 | 0.454 |
| <i>Microcebus myoxinus</i> | < 0.01 | < 0.01 | × | 0.773 | 0.068 | 0.447 |
| <i>Microcebus ravelobensis</i> | < 0.01 | < 0.01 | < 0.01 | × | 0.022 | 0.417 |
| <i>Microcebus rufus</i> | < 0.01 | < 0.01 | < 0.01 | < 0.01 | × | 0.147 |
| <i>Microcebus tavaratra</i> | < 0.01 | < 0.01 | < 0.01 | < 0.01 | < 0.01 | × |

I value above diagonal; p value below diagonal.

Significant p values indicate species occupy different niche spaces.

Hellinger's I (Warren *et al.*, 2008)

Table 23.3.

Niche overlap results using Schoener's D. Higher D values indicate greater niche overlap between species.

| Species | <i>M. griseorufus</i> | <i>M. murinus</i> | <i>M. myoxinus</i> | <i>M. ravelobensis</i> | <i>M. rufus</i> | <i>M. tavaratra</i> |
|--------------------------------|-----------------------|-------------------|--------------------|------------------------|-----------------|---------------------|
| <i>Microcebus griseorufus</i> | × | 0.476 | 0.221 | 0.056 | 0.260 | 0.043 |
| <i>Microcebus murinus</i> | < 0.01 | × | 0.554 | 0.236 | 0.303 | 0.210 |
| <i>Microcebus myoxinus</i> | < 0.01 | < 0.01 | × | 0.489 | 0.011 | 0.250 |
| <i>Microcebus ravelobensis</i> | < 0.01 | < 0.01 | < 0.01 | × | 0.002 | 0.235 |
| <i>Microcebus rufus</i> | < 0.01 | < 0.01 | < 0.01 | < 0.01 | × | 0.038 |
| <i>Microcebus tavaratra</i> | < 0.01 | < 0.01 | < 0.01 | < 0.01 | < 0.01 | × |

D value above diagonal; p value below diagonal.

Significant p values indicate species occupy different niche spaces.

Schoener's D (Schoener, 1968).

Figure 23.2

Graphical representation of the Maxent models for mouse lemur species. Each map represents the point-wise mean of the four replicate runs for each species. Warmer colors

(e.g., orange and red) indicate areas that are more suitable for species to occur, based on climate variables. Cooler colors (e.g., dark and light blue) indicate regions with poorly predicted conditions. Species include: (A) *Microcebus griseorufus*, (B) *M. murinus*, (C) *M. myoxinus*, (D) *M. ravelobensis*, (E) *M. rufus*, and (F) *M. tavaratra*.

Discussion

Our study supports the hypothesis that climate plays a significant role in determining mouse lemur distribution in Madagascar (Pearson and Raxworthy, 2009; Kamilar and Muldoon, 2010; Blair *et al.*, 2013). Our climate-based ENMs demonstrate significant predictive ability of occurrence records for all species except for *Microcebus murinus*. This is not surprising, given that genetic sampling has demonstrated fine-scale patterns of lineage divergence within regional populations of this geographically widespread species. The taxonomic grouping of *M. murinus* (*sensu lato*) likely encompasses multiple cryptic novel species (Weisrock *et al.*, 2010).

Our climate-based ENMs show possible overprediction in some areas in comparison with known ranges. Species may be absent in areas predicted by the model because there are geographic barriers that limit their dispersal into these areas. All *Microcebus* species are small-bodied primates (Kamilar *et al.*, 2012), and small taxa often have limited geographic ranges due to reduced dispersal ability across geographic barriers (Ayres and Clutton-Brock, 1992; Harcourt and Wood, 2012). Mouse lemurs in particular have been found to exhibit significant genetic differentiation at riverine boundaries (Olivieri *et al.*, 2007), supporting the idea that individuals dispersing across this type of barrier is limited. However, it should be noted that our data support the presence of *M. rufus* in the northeast (Figure 23.2E), where it is sympatric with other

newly described, distinct species that were excluded from our analysis based on minimum locality requirements.

Non-mutually exclusive phenomena may be at work. For instance, some mouse lemur species may actually have a broader distribution than currently known, as their small, nocturnal, and cryptic nature does not lend itself to easy identification. Our predictive models may provide direction for future surveys to focus on extending the geographic areas likely to be occupied by mouse lemur species.

In addition, species may be prevented from living in suitable habitat due to competitive exclusion from ecologically similar species. Competitive exclusion has been argued as an important influence of primate distributions at broad spatial scales (Ganzhorn, 1997; Lehman, 2006; Kamilar and Ledogar, 2011; Beaudrot *et al.*, 2013). Yet, this may also be an important factor at finer spatial scales within Madagascar. For example, *Microcebus murinus* and *M. griseorufus* occur sympatrically at sites within Andohahela Parcel 2 (xeric forest). *Microcebus murinus* also occurs in the ecotone that separates Parcel 2 and Parcel 1, but field researchers have not captured *M. murinus* within the boundaries of Parcel 1 (mesic forest) at Andohahela. The pattern of *Microcebus* spp. turnover along the ecotonal gradient could be due to a series of competitive exclusions: *M. griseorufus* may be best adapted to xeric vegetation formations, as conditions become more mesic, it is replaced by *M. murinus*, which in turn is replaced by *M. rufus* at the most humid end of the gradient (Rakotondranary *et al.*, 2011). Each species seems to have an evolutionary advantage within their respective vegetation type. However, recent studies have demonstrated that there is high intraspecific variation in morphology and physiology within mouse lemurs (Lahann *et al.*, 2006; Atsalis, 2007; Génin, 2008; Kobbe *et al.*, 2011). Interestingly, there is evidence

of hybridization between *M. murinus* and *M. griseorufus* at Andohahela despite clear ecological preferences (xeric vs. gallery forest; Hapke *et al.*, 2011). Hence, the ecological data currently available for these species do not provide any explanation for a selective advantage of one species over the other in different vegetation formations.

Two possible explanations exist for why *Microcebus murinus* was associated with a relatively poor ENM. This species may be an ecological generalist, being able to persist in a relatively broad range of climates and habitat types (Kamilar and Muldoon, 2010). If *M. murinus* is a generalist, then ENMs will not be able to predict their distribution with a high degree of confidence because their known occurrences are found in a wide range of environments. Assuming the broad niche of *M. murinus* is reflective of their biology, then this may have important implications for mouse lemur conservation. The relatively high level of discordance between their occurrence and the local climate and habitat may make this species better able to adapt to future shifts in climate (Dufresne *et al.*, 2013). Conversely, the relatively strong connection between climate and the distribution of other mouse lemur species suggest that these taxa will be susceptible to extinction or geographic range shifts under future models of climate change. Alternatively, the poor performing ENM for *M. murinus* may indicate that populations from this species should actually be elevated to full species. Molecular analyses using mtDNA and nDNA found clear genetic differentiation with *M. murinus*. In particular, *M. murinus* populations in southeastern Madagascar are completely distinct from western populations, with no evidence of gene flow (Weisrock *et al.*, 2010).

Finally, our study clearly demonstrates a significant amount of ecological (i.e., climatic) niche separation among all mouse lemurs examined. If the niche space occupied is indicative of species distinctness, then our results support the idea that each

of these six species are in fact truly separate species. Our findings also support previous work showing divergent climatic niches among mouse lemurs (as well as among many other lemur species) in a phylogenetic context (Kamilar and Muldoon, 2010). In addition, our results are concordant with a recent study demonstrating that rainfall and temperature were poor predictors of body mass variation in lemurs, including eight mouse lemur species (Kamilar *et al.*, 2012). The lemurs in our study are similar in body size, but the lack of niche overlap suggests that the particular environment in which they live does not significantly impact their body size. The lack of connection between climatic factors and body mass may at least be partly explained by use of daily torpor or hibernation that is known to occur in some cheirogaleid species (Blanco *et al.*, 2013; e.g., Blanco and Rahalinarivo, 2010). The use of these metabolic strategies may act as a buffer to the energetic constraints that mouse lemurs may have to face in different habitats.

In conclusion, we found that ecological niche models performed well for predicting the occurrence of mouse lemur species, with the exception of *M. murinus*. These results suggest that *M. murinus* is an ecological generalist or actually multiple species ~~that should be split into multiple taxa~~. In addition, we found that all of the mouse lemur species we examined exhibit little niche overlap, adding further support to recent genetic studies that have named new species.

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