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Anthropogenic and Climatic Effects on the Distribution of *Eulemur* Species: An Ecological Niche Modeling Approach

Jason M. Kamilar^{1,2,3} · Stacey R. Tecot⁴

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Abstract Several factors can influence primate distributions, including evolutionary history, interspecific competition, climate, and anthropogenic impacts. In Madagascar, several small spatial scale studies have shown that anthropogenic habitat modification affects the density and distribution of many lemur species. Ecological niche models can be used to examine broad-scale influences of anthropogenic impacts on primate distributions. In this study, we examine how climate and anthropogenic factors influence the distribution of 11 *Eulemur* species using ecological niche models. Specifically, we created one set of models only using rainfall and temperature variables. We then created a second set of models that combined these climate variables with three anthropogenic factors: distance to dense settlements, villages, and croplands. We used MaxEnt to generate all the models. We found that the addition of anthropogenic variables improved the climate models. Also, most Eulemur species exhibited reduced predicted geographic distributions once anthropogenic factors were added to the model. Distance to dense settlements was the most important anthropogenic factor in most cases. We suggest that including anthropogenic variables in ecological niche models is important for understanding primate distributions, especially in regions with significant human impacts. In addition, we identify several Eulemur species that were most

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affected by anthropogenic factors and should be the focus of increased conservation efforts.

Keywords Biogeography · Conservation · Extinction risk · Human impacts · Macroecology · Species distribution model

Introduction

An understanding of the factors impacting the diversity and distribution of primates can inform on past evolutionary processes, help identify current conservation challenges and priorities, and help prevent future biodiversity loss (Kamilar and Beaudrot 2013). Primate distributions are driven by many social and ecological factors including climate and habitat type (Muldoon and Goodman 2010; Reed and Fleagle 1995), intra- and interspecies competition (Kamilar and Guidi 2010; Kamilar and Ledogar 2011), predator–prey interactions (Farris *et al.* 2014), geographic features (Goodman and Ganzhorn 2004), and evolutionary history (Kamilar 2009; Lehman 2006), as well as an interaction between several factors, including climate change (Wilmé *et al.* 2006). Increasingly, anthropogenic factors alter landscapes and reduce the effective space available for species to exist, and are also known to impact the distribution of species (Irwin *et al.* 2010).

Climate and habitat characteristics are among the strongest evolutionary forces acting on species. In Madagascar, habitat alteration affects the density and distribution of many lemur species (Irwin 2006; Johnson and Overdorff 1999). The structural characteristics and reproductive schedule of trees may impact not only an animal's direct nutrient intake, but also its range and travel routes (Grassi 2001; Overdorff 1993), locomotion (Dagosto and Yamashita 1998), safety from predators (Curtis *et al.* 1999; Miller 2002), and activity pattern (Curtis *et al.* 1999). Habitat alteration can also influence behavior by modifying predator–prey interactions. For example, in northeastern Madagascar (Farris *et al.* 2014), lemurs are less active in fragmented landscapes where they are exposed to nonnative predators and humans, in comparison with lemurs in contiguous forest that have more interactions with endemic predators. Studies focused on individual species report that some taxa thrive in altered landscapes, e.g., *Hapalemur griseus* (Grassi 2001), but anthropogenic impacts are generally negative (Irwin *et al.* 2010).

Ecological niche modeling is another approach to understand better how anthropogenic factors influence primate distributions. Ecological niche models, i.e., species distribution models, most commonly use climate variables, such as various measures of rainfall and temperature, combined with the known occurrence of species to estimate where species should be distributed based on their known niche space (Elith *et al.* 2006; Kamilar and Beaudrot 2015; Phillips *et al.* 2006). A variety of topics can be addressed using this approach, including investigating patterns of speciation (Blair *et al.* 2013), taxonomy (Raxworthy *et al.* 2007), species diversity (Kamilar *et al.* 2015), and niche diversity (Johnson *et al.* 2015), and it is possible to model shifts in species ranges resulting from future climate change (Thorne *et al.* 2013). In many cases, these models overpredict known species distributions because other factors that may influence distribution patterns are not considered, such as geographic barriers and biotic interactions, though recent work is attempting to address some of these issues (Boulangeat *et al.* 2012; Kissling *et al.* 2012).

Anthropogenic impacts are another factor that can have an important impact on species distributions but have rarely been used in distribution modeling studies (*cf.* Junker *et al.* 2012). Anthropogenically altered landscapes are typically quantified according to measures of their biodiversity (e.g., richness and diversity), and human activity (e.g., distance to edge, hunting pressure, distance to village). However, the type of human settlement is not often considered, though human-use activities likely differ in urban areas, villages, and agricultural lands.

The genus *Eulemur* is ideal for modeling the impacts of climate and anthropogenic impacts on species distributions. *Eulemur* is a diverse clade consisting of 12 species (Markolf *et al.* 2013). They live in pairs and larger social groups and exhibit different levels of group cohesion (Kappeler and Fichtel 2015). They are known to be ecologically flexible primates with great dietary diversity (Donati *et al.* 2007; Ossi and Kamilar 2006), and they can distribute their activity throughout a 24-h period, i.e., cathemerality, and do so to varying degrees (Curtis and Rasmussen 2006; Tattersall 1987). The geographical distribution of *Eulemur* is broad, and they occupy all types of forest in Madagascar (Tattersall and Sussman 1998). At the same time, pair-living and group-living *Eulemur* appear to suffer when living in degraded habitat (Balestri *et al.* 2014; Tecot 2013). The density and distribution of *Eulemur* has been recorded in a number of studies throughout the island (Brown and Yoder 2015).

Conservation biology research focused on Malagasy primates is especially important because Madagascar is a biodiversity hotspot with astounding species richness and endemism (Goodman and Benstead 2005; Myers *et al.* 2000). Yet, lemurs were recently named the most threatened group of mammals on the planet, with an increase from 74% to 94% of species threatened with extinction, largely due to the continued loss of forest (Schwitzer *et al.* 2014). Habitat degradation outside of protected areas is widespread, and protected areas, e.g., national parks, are impacted by illegal activities as well (Schwitzer *et al.* 2014). Madagascar's lemurs have faced extinction in the past; 17 subfossil lemur species have gone extinct subsequent to the arrival of humans on the island (Burney and Flannery 2005; Burney and MacPhee 1988). This loss was at least in some part due to human hunting activity and climate change (Crowley 2010), which may have resulted in reduced genetic diversity of these megafauna (Kistler *et al.* 2015). Today, habitat fragmentation appears to play a primary role in reducing lemur species richness (Irwin *et al.* 2010).

In this study, we used an ecological niche modeling approach to examine the effect of climatic and anthropogenic factors on *Eulemur* distributions. In particular, we compared models using only climate variables to those that used climate and anthropogenic factors. We examined three types of anthropogenically modified habitats: dense settlements, i.e., urban areas; villages; and croplands. If anthropogenic factors impact distributions of *Eulemur*, then we predicted that adding anthropogenic variables to climate models would result in an increased probability that species are absent from a particular location, thereby reducing the total predicted distribution of species. In addition, we expected that the addition of anthropogenic variables will increase the predictive power of the model compared with using climate variables only.

Methods

Data Collection

We collected data for 11 *Eulemur* species (Markolf and Kappeler 2013; Appendix S1: *E. albifrons, E. cinereiceps, E. collaris, E. coronatus, E. flavifrons, E. fulvus, E. macaco* (sensu stricto), *E. rubriventer, E. rufifrons, E. rufus* (sensu stricto), *E. sanfordi.* This dataset contained known localities of *Eulemur* used in Brown and Yoder (2015). Brown and Yoder (2015) present multiple versions of their data and we used only their "vetted and rarefied" dataset. One advantage of this dataset is that it contains only localities that are \geq 5 km apart from each other, thereby reducing the effects of spatial autocorrelation in the subsequent niche models. Additional details about these data can be found in Brown and Yoder (2015).

We used six climate variables to characterize the climatic niche space occupied by species, and these variables served as the basis for the species distribution models: 1) precipitation of the coldest quarter; 2) precipitation of the driest quarter; 3) temperature annual range; 4) minimum temperature of coldest month; 5) temperature seasonality (standard deviation \times 100); 6) isothermality, defined as mean diurnal range [mean of monthly (max temperature – min temp)] divided by temperature annual range. All of the climate variables were obtained from the Worldclim database (Hijmans *et al.* 2005). These variables were chosen for several reasons: They should well represent the range of climatic and habitat conditions experienced by *Eulemur* (Kamilar and Muldoon 2010); they correlate less strongly to each other than other measures of rainfall and temperature, therefore reducing the degree of multicollinearity in the models; quantifying rainfall and temperature variation should be related to lemur physiology and overall biology (Dewar and Richard 2007; Wright 1999); and these variables were used in a recent species distribution modeling study of *Eulemur* by Blair *et al.* (2013).

We used three variables to quantity possible anthropogenic effects on Eulemur distributions, distance to 1) dense settlements, 2) villages, and 3) croplands. We obtained these data from the Anthropogenic Biomes of the World (version 2) produced by the NASA Socioeconomic Data and Applications Center (Ellis et al. 2010, 2013). The original dataset was a GeoTIFF file at a 5 arc-minute resolution that assigned a single anthropogenic biome type to each pixel in the map. The biomes are based on data from the year 2000 and are defined by three main factors: population size (urban, nonurban), land use (percent area of pasture, crops, irrigation, rice, urban land), and land cover (percent area of trees and bare earth). Each broad biome classification was composed of multiple subcategories, e.g., rice villages, irrigated villages, that were collapsed for analysis. This was done to reduce the number of correlated predictor variables. Additional methodological details can be found in the original sources referenced previously. We used ArcMap and the Spatial Analyst toolbox to create three distance rasters from this original GeoTIFF file, with each raster representing one of the three anthropogenic biomes. We accomplished this by first reclassifying the original raster to three new rasters, with each representing one of the anthropogenic biomes. Then we used the Euclidian distance function to create the distance rasters.

Data Analysis

We used MaxEnt (version 3.3.3k) (Phillips and Dudik 2008; Phillips *et al.* 2006) to build species distribution models. We constructed two models for each species, one using climate variables only and a second using climate and anthropogenic variables. MaxEnt has become the most commonly used algorithm for species distribution modeling when only known occurrence data are used (as opposed to using both known occurrences and absences). Although methods that do not incorporate known absences have some limitations (Yackulic *et al.* 2013), a comparison of species distribution methods showed that MaxEnt performs as well or better than other models (Elith *et al.* 2006). In addition, this approach does not require assumptions about the processes driving the ecological patterns nor does it make assumptions about the forms of the relationships between variables (Frank 2009; Harte *et al.* 2008).

For each model, we set 75% of the species' known localities as training data and 25% of the localities as test data. We used three different regularization multipliers (values of 1, 2, and 3) to examine the possible effects of model overfitting (Radosavljevic and Anderson 2013). The regularization multipliers had a minimal effect on the model outcomes, so we only present the results of the models using a value of 1. In addition, we used a fourfold cross-validation procedure that randomly splits the occurrence data into equal sized groups (Blair *et al.* 2013; Peterson *et al.* 2011). Using this method is important, especially when small datasets are present, because it uses all data for model validation. The fourfold data partitioning produces four models per dataset (climate only and climate + anthropogenic variables) per species. Other model options were set to the recommendations presented by the MaxEnt authors (Phillips *et al.* 2006; Phillips and Dudık 2008).

We judged model performance using two criteria. The first is the 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 (because the null expectation is based on a 50% absence and 50% presence probability). AUC values >0.5 indicate improved model performance, with values of 1.0 indicating a model with perfect predictive ability. Following Hosmer and Lemeshow (2000), we considered AUC values of 0.7–0.8 as an acceptable prediction, 0.8–0.9 as excellent, and >0.9 as outstanding. An AUC value is associated with each fold. Therefore, we present the mean test AUC for each dataset of each species, as well as the standard deviation for the models. Second, we used a binomial test of omission under a minimum training presence threshold to calculate the statistical significance of each model's prediction (Anderson *et al.* 2002). AUC values can be affected by the niche space occupied by a species. Species occupying relatively narrow niches as defined by the predictor variables usually have higher AUC values compared to species occupying broad niches.

We used two approaches to evaluate the effect of anthropogenically modified habitats on distributions of *Eulemur*. First, we calculated the percent contribution of each predictor variable for each model. If anthropogenic variables are important predictors of species distributions, then they should show relatively high values compared with climate variables. The percent contribution values we present are the means across the fourfold runs for each model. Second, for each model, we calculated the predicted species range size based on two presence probability cutoff values, 75%

Species	$N^{\rm d}$	Dataset	Mean Test AUC	Test AUC SD	Omission rate-fold 1 ^b	Omission rate-fold 2 ^b	Omission rate-fold 3 ^b	Omission rate-fold 4 ^b
E. albifrons	28	Climate	0.936	0.019	0.143, P = 0.0005	0, P < 0.0001	0.143, P = 0.0004	0, P < 0.0001
E. cinereiceps	12	Climate	0.899	0.038	0.667, P = 0.287	0, P = .0038	0, P = 0.0031	1, P = 1.000
E. collaris	27	Climate	0.948	0.022	0, P < 0.0001	0.143, P = 0.0001	0.286, P = 0.0026	0, P < 0.0001
E. coronatus	15	Climate	0.975	0.012	0.500, P = 0.0131	0.250, P = 0.0004	0, P < 0.0001	0, P = 0.0001
E. flavifrons	13	Climate	0.994	0.002	0, P < 0.0001	0, P < 0.0001	0, P < 0.0001	0.333, P = 0.0003
E. fulvus	61	Climate	0.787	0.016	0, P = 0.0002	0.067, P = 0.0010	0, P = 0.0010	0.133, P = 0.0178
E. macaco (sensu stricto)	22	Climate	0.974	0.008	0.333, P < 0.0001	0, P < 0.0001	0.200, P < 0.0001	0, P < 0.0001
E. rubriventer	40	Climate	0.926	0.016	0, P < 0.0001	0, P < 0.0001	0, P < 0.0001	0.300, P = 0.0004
E. rufifrons	82	Climate	0.895	0.005	0, P < 0.0001			
E. rufus (sensu stricto)	30	Climate	0.923	0.009	0, P < 0.0001	0.125, P < 0.0001	0, P < 0.0001	0.143, P < 0.0001
E. sanfordi	Π	Climate	0.970	0.009	0, P = 0.0001	0, P = 0.0002	0.333, P = 0.0051	0, P = 0.0024
E. albifrons	28	Climate + Anthro	0.935	0.032	0.429, P = .0004	0, P < 0.0001	0, P < 0.0001	0.167, P = 0.0004
E. cinereiceps	12	Climate + Anthro	0.930	0.024	0, P = 0.0016	0, P = 0.0033	0, P = 0.0018	0.333, P = 0.0542
E. collaris	27	Climate + Anthro	0.981	0.008	0, P < 0.0001	0.167, P < 0.0001	0, P < 0.0001	0, P < 0.0001
E. coronatus	15	Climate + Anthro	0.983	0.005	0.250, P = 0.0001	0.500, P = 0.0032	0, P < 0.0001	0, P < 0.0001
E. flavifrons	13	Climate + Anthro	0.997	0.002	0, P < 0.0001	0.667, P = 0.0149	0, P < 0.0001	0.333, P = 0.0001
E. fulvus	61	Climate + Anthro	0.855	0.01	0.067, P < 0.0001	0, P < 0.0001	0.133, P = 0.0001	0, P < 0.0001
E. macaco (sensu stricto)	22	Climate + Anthro	0.989	0.003	0.200, P < 0.0001	0, P < 0.0001	0, P < 0.0001	0, P < 0.0001
E. rubriventer	40	Climate + Anthro	0.948	0.009	0, P < 0.0001	0.100, P < 0.0001	0.100, P < 0.0001	0, P < 0.0001
E. rufifrons	82	Climate + Anthro	0.886	0.020	0, P < 0.0001	0, P < 0.0001	0, P < 0.0001	0.150, P < 0.0001
E. rufus (sensu stricto)	30	Climate + Anthro	0.943	0.019	0, P < 0.0001	0, P < 0.0001	0, P < 0.0001	0.286, P = 0.0003
E. sanfordi	Ξ	Climate + Anthro	0.979	0.006	0.333, P = 0.0032	0, P < 0.0001	0.333, P = 0.0029	0.500, P = 0.0635

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^a Total number of localities used to build model. ^b Binomial omission test under a minimum training presence threshold.

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Species	Precipitation of driest quarter	Temperature seasonality	Isothermality	Min temperature of coldest month	Precipitation of coldest quarter	Temperature annual range	Distance to dense settlement	Distance to villages	Distance to cropland
E. albifrons ^a	62	26.2	6.5	0.4	4.9	0			
E. albifrons ^b	44.9	8.8	5.9	0.1	3.7	0.1	9.2	20.7	6.7
E. cinereiceps ^a	0.0	43.8	4.6	0	0.4	50.3			
E. cinereiceps ^b	0	31.6	3.7	1	0	62.7	0.9	0	0.1
E. collaris ^a	50.7	2.5	5.5	0.4	17.9	23			
E. collaris ^b	22.8	0.2	0.6	3.2	0	0.2	41.6	30.5	0.8
E. coronatus ^a	0	2.2	7.4	0	0	90.4			
E. coronatus ^b	0	21	1	0	0.2	48.5	0.3	0	29
E. flavifrons ^a	16	10	73.5	0	0.5	0			
E. flavifrons ^b	7.4	1.5	6	1.3	10.2	0	70.5	0	0
E. fulvus ^a	8.3	5.7	11.1	8.5	23.1	43.3			
E. fulvus ^b	1.3	1	0.9	1.7	7.3	16.7	27.2	8.8	35.2
E. macaco ^a	12.1	63.7	0.4	0.3	23.2	0.4			
E. macaco ^b	0.3	15.3	0	0	5.2	0	79.2	0	0
E. rubriventer ^a	30.2	0.4	0.1	30.1	1.5	37.8			
E. rubriventer ^b	27.6	0	0.8	25.3	3.4	17.3	17.8	4.4	3.4
E. rufifrons ^a	9.7	17.8	22.7	21.7	20.2	8			
E. rufifrons ^b	16.3	12.9	20.5	19.3	19	3.6	0.5	4.8	3.1
E. rufus ^a	59	8.2	2.9	25.7	3.4	0.9			
E. rufus ^b	37.3	18.9	3.2	13.7	0.5	0	22.1	0.6	3.7
E. sanfordi ^a	0	1.2	17.6	0	0	81.2			
E. sanfordi ^b	0	35.7	13.7	0	0	32.2	0	0.2	18.3

Table II Variable percent contribution values associated with MaxEnt models

^a Model using climate variables only. ^b Model using climate and anthropogenic variables.

Values are averaged across replicates for each species.

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Species	Climate ^a	Climate + Anthro ^a	% change in range size from anthropogenic impacts ^a	Climate ^b	Climate + Anthro ^b	% change in range size from anthropogenic impacts ^b
E. albifrons	6876	6595	-4.1	1514	4065	168.5
E. cinereiceps	9990	11,568	15.8	4973	5816	17.0
E. collaris	8714	3589	-58.8	4000	2184	-45.4
E. coronatus	4562	3957	-13.3	1297	1406	8.4
E. flavifrons	1492	1124	-24.7	1254	497	-60.4
E. fulvus	12,995	8822	-32.1	6249	3979	-36.3
E. macaco (sensu stricto)	3049	2378	-22.0	151	195	29.1
E. rubriventer	7525	4692	-37.6	2227	2616	17.5
E. rufifrons	13,968	9276	-33.6	6703	4779	-28.7
E. rufus (sensu stricto)	7524	6141	-18.4	2227	2573	15.5
E. sanfordi	11,244	5362	-52.3	6140	3330	-45.8

Table III Predicted geographic range of *Eulemur* species based on a climate model vs. climate and anthropogenic impact model

Predicted geographic range values are in square kilometers. Species in bold are most negatively affected by anthropogenic impacts. Negative percentages indicate that anthropogenic impacts reduce species range size. Range size calculations are based on each pixel representing 21.6225 km^2 .

^a Based on 70% probability that species is present in each pixel.

^b Based on 75% probability that species is present in each pixel.

and 70%. We used two threshold criteria because there is no single method that best provides the correct threshold value and the specific goal of a study is an important consideration for setting a particular threshold (Jiménez-Valverde and Lobo 2007; Liu *et al.* 2005). In addition, we felt it was important to use both 75% and 70% values because many pixels exhibited probabilities between these two values. We quantified the number of pixels displaying these presence probabilities and multiplied this value by 21.62 km², which is the estimated area of each map pixel corresponding to our raster resolution. For each species, we compared the predicted range size of the climate only models vs. the climate + anthropogenic variable models.

Results

We found that the climate only and climate plus anthropogenic factors models performed well for most species. For the climate models, mean test AUC values ranged from 0.787 for *Eulemur fulvus* to 0.994 for *E. flavifrons* (Table I), with a mean value of

Fig. 1 Species distribution models produced for *Eulemur albifrons* (**A**, **B**) and *E. cinereiceps* (**C**, **D**) using climate variables (**A**, **C**) and climate + anthropogenic factors (**B**, **D**). Warmer colors indicate a greater certainty of species being present. Cooler colors indicate a greater certainty of species being absent. Green pixels indicate the areas of greatest uncertainty.

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1 0.92 0.85 0.77 0.69 0.62 0.54 0.46 0.38 0.31 0.23 0.15 0.08



1 0.92 0.85 0.77 0.69 0.62 0.54 0.46 0.38 0.31 0.23 0.15 0.08 0

Fig. 2 Species distribution models produced for *Eulemur collaris* (A, B) and *E. coronatus* (C, D) using climate variables (A, C) and climate + anthropogenic factors (B, D). Warmer colors indicate a greater certainty of species being present. Cooler colors indicate a greater certainty of species being absent. Green pixels indicate the areas of greatest uncertainty.

0.930 across all species. Binomial tests for all of the fourfolds were significant for 10 of the 11 species. One species, *E. cinereiceps*, exhibited significant results for three of the fourfolds.

The mean test AUC values were expectedly higher (due to the additional predictor variables) for the models that included both climatic and anthropogenic variables and ranged from a minimum of 0.855 for *Eulemur fulvus* to a maximum of 0.997 for *E. flavifrons*, with an average value of 0.948 across all species. Nine of 11 species exhibited statistically significant binomial tests for all of the fourfolds. Two species, *E. cinereiceps* and *E. sanfordi*, exhibited significant results for three of the four folds.

Different climate variables best predicted the distribution of *Eulemur* species based on the percent contribution values for the climate-only models (Table II). The precipitation of the driest quarter was the most important predictor of *E. albifrons*, *E. collaris*, and *E. rufus* distributions. Temperature seasonality was the best predictor of *E. macaco*. Another measure of temperature variation, temperature annual range, was the most important climate variable explaining the range of *E. ciniercips*, *E. coronatus*, *E. fulvus*, *E. rubriventer*, and *E. sanfordi*. Finally, isothermality best explained the modeled distribution of two species, *E. rufifrons* and *E. flavifrons*.

We found interesting results when anthropogenic variables were combined with climatic factors in the species distribution models (Table II). The sum of the contribution values for the three anthropogenic variables was greater than 70% for *E. collaris*, *E. flavifrons*, *E. fulvus*, and *E. macaco*. In addition, *E. albifrons*, *E. coronatus*, *E. rubriventer*, and *E. rufus* exhibited summed values >25%. The remaining species exhibited values <20%. The importance of the specific anthropogenic variables also differed. The across-species mean contribution value for the distance to dense settlement variable was 24.5%. In contrast, the same measurement was 9.1% for distance to cropland and 6.4% for distance to villages. Distance to dense settlement was the most important anthropogenic predictor for six species, whereas distance to villages was the best anthropogenic predictor for three species, and distance to villages was the best predictor for two species.

Compared with the models using climate variables only, most *Eulemur* species exhibited smaller predicted distributions when anthropogenic factors were considered in combination with climate (Table III and Figs. 1, 2, 3, 4, 5, and 6). This was especially true when we used a 70% probability as the criterion for accepting a predicted species presence. The average predicted distribution across *Eulemur* species based on climate alone was 7994 km² compared to 5773 km² when anthropogenic effects were include in the model (a range reduction of 27.8%). Ten of the 11 species showed smaller total range sizes for the climate + anthropogenic models compared with using climate variables alone (*E. cinereiceps* was the only exception). The amount of range reduction varied from 4.1% for *E. albifrons* to 58.8% for *E. collaris*. In addition, the mean predicted geographic ranges of species decreased when accounting for anthropogenic effects and using 75% as the accepted probability level of a species' presence. Climate-only models produced a mean predicted species distribution of 3340



Fig. 3 Species distribution models produced for *Eulemur flavifrons* (A, B) and *E. fulvus* (C, D) using climate variables (A, C) and climate + anthropogenic factors (B, D). Warmer colors indicate a greater certainty of species being present. Cooler colors indicate a greater certainty of species being absent. Green pixels indicate the areas of greatest uncertainty.

 km^2 compared to 2858 km^2 for climate + anthropogenic models. Yet, we obtained more mixed results when examining individual species. Five of the 10 species exhibited slightly greater predicted ranges when anthropogenic effects were included in the model, one species exhibited a noticeably greater increase (*E. albifrons*), and five species exhibited decreased ranges. Only one of the 11 species we examined, *E. ciniercips*, showed a consistent increase in predicted range size when anthropogenic effects were included in the distribution model. This increase was quite modest, at just over 16%.

Discussion

Using a species distribution modeling approach, we found that both climate-only and climate and anthropogenic models are excellent or outstanding at predicting distributions of *Eulemur*. Importantly, we found that the geographic ranges of several *Eulemur* species are influenced by anthropogenic factors. In particular, five species (*E. collaris, E. fulvus, E. flavifrons, E. rufifrons,* and *E. sanfordi*) exhibited substantially reduced distributions once anthropogenic impacts are accounted for in the model. In addition, we found that the distance to dense settlements contributed the most to explaining distributions of *Eulemur*, followed by distance to cropland, and then distance to villages. Interestingly, there was evidence to support the idea that one species, *E. cinereiceps*, exhibited an increased modeled distribution once anthropogenic effects were quantified. A detailed visual examination of its predicted distribution (Fig. 1C), however, yields only slight differences between the two models.

Our findings broadly support prior research examining human impacts on primate distributions and extinction risk. On a global scale, Harcourt and Parks (2003) found that human population density was higher within the geographic range of threatened primate taxa compared with low-risk species. Junker et al. (2012) showed that the suitable environmental conditions of African great apes from the 1990s to the 2000s were negatively impacted by human-modified landscapes and the intensity of these impacts varied by species. In addition, Brown and Yoder (2015) found that lemur ranges are likely to shift in accordance with future climate change. Yet, similar to our results, the degrees to which lemur ranges shift vary across species. About 60% of the 57 species they examined will experience range contractions, yet other taxa will experience range stability or range increases. These differential impacts are independent of phylogeny, with closely related taxa, e.g., Eulemur spp., experiencing very different responses to climate change. Although anthropogenic impacts are usually detrimental to primates, there is some evidence suggesting positive effects are possible, at least on a limited basis. For lemurs, Overdorff (1991) noted that some Eulemur species will use fruit tree groves when forest food resources are scare.

Several mechanisms may be responsible for the negative impact of anthropogenically modified areas on distributions of *Eulemur*. At a basic level, most types of



Fig. 4 Species distribution models produced for *Eulemur macaco* (A, B) and *E. rubriventer* (C, D) using climate variables (A, C) and climate + anthropogenic factors (B, D). Warmer colors indicate a greater certainty of species being present. Cooler colors indicate a greater certainty of species being absent. Green pixels indicate the areas of greatest uncertainty.

anthropogenically modified areas are associated with reduced habitat availability. *Eulemur* are forest-dwelling primates, and as such are negatively impacted by forest modification, degradation, and loss. Dense settlements, i.e., urban areas, in particular are likely to be associated with the complete elimination of natural habitats, thereby resulting in the extirpation of *Eulemur* species (and other lemurs). Even in areas with less extreme habitat destruction, forest fragmentation is widespread throughout Madagascar (Harper *et al.* 2007). Most of this widespread habitat alteration is due to large-scale, and often illegal, industrial logging and mining (Gore *et al.* 2013; Horning 2012).

There is increasing evidence showing that *Eulemur* species are negatively impacted by habitat disturbance. Recent research examining hormone levels supports the idea that living in degraded forest impacts the physiology of some *Eulemur* species. Balestri *et al.* (2014) found that *E. collaris* in degraded forest exhibited higher fecal glucocorticoid metabolite levels compared with individuals living in nearby intact forest. In addition, a study focused on *E. rubriventer* (Tecot 2013) found that individuals in disturbed habitat did not respond behaviorally or physiologically to seasonal changes in food availability and climate, in contrast with those in undisturbed forest. Groups in disturbed forest reproduced out of season and had much higher infant mortality rates as well, which could lead to a long-term population decline (Tecot 2008, 2010).

The anthropogenic variables we examined in our analysis may also be related to hunting intensity. Being in close proximity to anthropogenic areas, especially villages and croplands, may increase the likelihood of being hunted. Hunting of lemurs has been increasing in recent years, possibly due to the nutritional needs of local people (Golden *et al.* 2011; Jenkins *et al.* 2011). *Eulemur* species are known to be hunted throughout the island (García and Goodman 2003; Golden 2009; Johnson and Overdorff 1999). Additional research is necessary to determine how increased hunting intensity may impact *Eulemur* density and distribution.

Another anthropogenically mediated mechanism that may negatively impact populations of *Eulemur* is pathogens. Several studies have shown that pathogen transmission between humans and wild nonhuman primates occurs in many areas (Köndgen *et al.* 2008; Nunn 2012). In particular, lemurs in anthropogenically disturbed areas of Ranomafana National Park exhibited higher prevalence rates of gastrointestinal helminths, protozoa (Rasambainarivo *et al.* 2013; Wright *et al.* 2009), and disease-causing enterobacteria (Bublitz *et al.* 2014), but the effects on *Eulemur* species have not been studied. It is still unknown whether direct contact with humans or human-associated animals, e.g., cattle, rodents, is the source of these pathogens.

Future work should focus on explicitly examining the possible biological traits that allow *Eulemur cinereiceps* to be less affected by anthropogenic impacts (at least in terms of their modeled geographic distribution), while most other species show clear negative impacts. *Eulemur* are known to be ecologically flexible primates (Donati *et al.* 2007; Ossi and Kamilar 2006), including showing a relatively high degree of variation in activity pattern, diet, activity budget, and social organization. Body size is



Fig. 5 Species distribution models produced for *Eulemur rufifrons* (A, B) and *E. rufus* (C, D) using climate variables (A, C) and climate + anthropogenic factors (B, D). Warmer colors indicate a greater certainty of species being present. Cooler colors indicate a greater certainty of species being absent. Green pixels indicate the areas of greatest uncertainty.

often an important predictor of rarity and extinction risk, though *Eulemur* species do not vary a great deal in this trait (Kamilar *et al.* 2012). Previous work has shown that some leaf eating primates are more resistant to habitat disturbance (Johns and Skorupa 1987; Kamilar and Paciulli 2008; Oates *et al.* 1990) compared with frugivorous species. Therefore, investigating dietary variation across species, as well as the degree of seasonal variation in diet, may be a fruitful avenue of exploration. Interestingly, a recent study of population size and genetic diversity of *E. cinereiceps* lends support to our results. Brenneman *et al.* (2012) unexpectedly found evidence of gene flow across intact and fragmented forests, even those separated by anthropogenic grasslands. In addition, they did not find a statistically significant decline in the genetic diversity of populations living in fragmented habitats. These results may indicate that *E. cinereiceps* is more resilient to anthropogenic impacts compared with other *Eulemur* species. An additional factor to consider is the timing of anthropogenic impacts. Populations of *Eulemur* that have only recently been exposed to anthropogenic factors may not currently show reductions in population size, genetic diversity, or geographic range



Fig. 6 Species distribution models produced for *Eulemur sanfordi* (**A**, **B**) using climate variables (**A**) and climate + anthropogenic factors (**B**). Warmer colors indicate a greater certainty of species being present. Cooler colors indicate a greater certainty of species being absent. Green pixels indicate the areas of greatest uncertainty.

size because of time lag effects. Our anthropogenic variables were based on data from the year 2000, whereas the localities of *Eulemur* are reflecting current or recently known locations. Therefore, this discrepancy in temporal sampling may introduce additional error into our models and underestimate the impact of anthropogenic factors on some species.

Additional factors that may influence distributions of *Eulemur* should also be considered in the future. Biotic interactions, either among congeners, other lemur taxa, and/or other potential competitors could influence biogeography of *Eulemur* (Ganzhorn 1997; Kamilar and Ledogar 2011) by reducing their geographic ranges. Also, geographic barriers, such as rivers, may limit species ranges through reduced dispersal (Ayres and Clutton-Brock 1992; Harcourt and Wood 2012). The modeled distribution of species may change if these factors are explicitly quantified.

We hope that our approach can be useful for setting conservation priorities in the face of growing anthropogenic impacts on Madagascar. Conservation personnel and funding are limited and our findings suggest that some *Eulemur* are differentially affected by human-modified habitats. Conserving *Eulemur* species, as well as other lemurs (especially frugivorous species), serves to not only preserve primate diversity on Madagascar, but also acts as a mechanism to maintain the extreme biodiversity on the island (Wright *et al.* 2011). The importance of lemurs for maintaining plant diversity was nicely demonstrated for *E. rubriventer*, which was shown to be an important seed disperser of a long-lived Malagasy rainforest tree species, *Cryptocarya crassifolia* (Razafindratsima and Dunham 2015). In sum, the results of our study should be combined with other information (Schwitzer *et al.* 2013) to create more holistic conservation plans.

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