



The importance of deforestation and climate change in shaping lemurs' distributions and identifying their areas of climatic refuges



Mémoire de stage de Master 2 Biodiversité, Ecologie et Evolution (BEE) finalité Gestion Adaptative de la Biodiversité (GABI)

Réalisé par Corentin Knoploch au sein de l'association Nitidae

Encadré Clovis Grinand (Nitidae) et Ghislain Vieilledent (CIRAD)



Année universitaire 2018-2019



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Sommaire

Liste des figures	6
Liste des tableaux	6
Liste des annexes	6
Introduction	7
Materials and methods	10
Species and climate data	10
Species occurrences	10
Climatic data	10
Climate change scenarios	11
Forest cover and deforestation maps	11
Protected area network	12
Species distribution modelling	12
Algorithm choice	13
Algorithm parameters	13
BIOMOD's modelling options	13
Accuracy metrics	14
Committee averaging	14
Data Analysis	14
Species' dispersal capabilities	14
Species distribution area change	15
Core range shift	16
Identifying areas of high conservation interest	16
Assessing climate change and deforestation impacts	17
Identifying refuges threatened by deforestation	17
Results	18
Dataset preparation	18
Modelling process	18
Species' responses	19
Community response	22
Identifying refuges	24
Discussion	27
Climate change and deforestation effect on lemurs	27
Disentangling the role of climate change and deforestation	28
Conservation implications	29
Conclusion	31
References	32
Annexes:	37
Abstract	43
Résumé	43

Liste des figures

Figure 1: Lemurs species classified from their response to climate change and deforestation	n 20
Figure 2 : Main areas of species range shift from current to future SDA	21
Figure 3: Predicted species richness maps.	22
Figure 4: Predicted number of species gained and lost	23
Figure 5: (a) Smoothed color density plot obtained by plotting future irreplaceability aga	ainst
species richness. (b) Future irreplaceability plotted against species turnover	25
Figure 6: Areas identified as refuges and their threat from deforestation	26

Liste des tableaux

Table 1: Different assumptions combinations used in this study for future ensemble n	nodels 15
Table 2: Number of observations classified by lemurs' families	
Table 3 : Minimum, maximum and median values for three accuracy metrics	19
Table 4: Mixed models outputs obtained from modelling the effect of climate ch	ange and
deforestation	
Table 5: Predicted percentage of habitat lost and total richness	
Table 6: Refuges characteristics	

Liste des annexes

Annex I: Number of observations for each lemur species	37
Annex II: Predicted impact on SDA for every scenario combination under five classes responses	of 39
Annex III: Cumulative histogram of species lost	40
Annex IV: Predicted species richness maps from both current	41
Annex V: Predicted number of species lost under the 8.5, full dispersal, no deforestati scenario	on 42

Introduction

One of the factors leading to Madagascar identification as a high priority conservation hotspot is its exceptional species richness and its high concentration of endemic species (Myers et al. 2000). With more than 80% of vertebrate being only found on this island, 83% of plants and more than 50% of flying animals (Goodman & Benstead 2005), Madagascar's endemism levels are almost unparalleled across the whole planet. At the largest scale, this high level of endemism can be explained partially from the fragmentation of the Gondwanan continent into Africa, Australia, Antarctica, South America, Madagascar, and India. These episodes, ranging from 175 to 85 million years ago (Ali & Aitchison 2008), progressively led to the isolation of Madagascar and are associated with multiple event of vicariance (Noonan & Chippindale 2006; Toussaint et al. 2016). This large scale endemism may also be explained by different event of dispersion from the African continent to Madagascar since their separation (Yoder & Nowak 2006; Pirie et al. 2015). Although, this isolation doesn't provide any explanation for its high level of microendemism. Numerous hypotheses have been proposed to explain the processes that created Madagascar's taxa exceptional radiation. Among them are the diversity, variability and unpredictability of Madagascar climate (Dewar & Richard 2007), the role of watershed during previous glaciation episodes (Wilmé 2006) or river acting as barrier (Pastorini et al. 2003). But no mechanism appears as universal and instead multiple processes acting together may be held responsible (Pearson & Raxworthy 2009; Vences et al. 2009).

Despite understanding every mechanism underlying this exceptional level of local endemism, species distribution patterns over the island have been relatively well studied (Raxworthy *et al.* 2003; Brown *et al.* 2016) and used to propose conservation policies (Pearson *et al.* 2007; Kremen *et al.* 2008). But, as past climate shaped Madagascar biodiversity evolution and distribution, climate change is also expected to greatly impact its future (Hannah *et al.* 2008). Thus, the importance of exploring future species distribution patterns in order to evaluate the efficiency of protected areas, or identify new ones, has been addressed multiple times (Hannah *et al.* 2008; Coetzee *et al.* 2009; Vieilledent *et al.* 2018).

Examples showing the effects of climate change on species have long been presented and prove to be coherent across different taxonomic group (Parmesan & Yohe 2003; Rossi *et al.* 2019). In Madagascar, important climate change are to be expected, with temperature increasing by 1.1 to 2.6°C before the end of the century (Hannah *et al.* 2008) and rainfall regime predicted to change importantly across the whole island (Tadross *et al.* 2008). In the light of these assessments, several studies have attempted to anticipate species responses across different Malagasies taxonomic group, like birds (Andriamasimanana & Cameron 2013), baobabs (Vieilledent *et al.* 2013) and lemurs (Brown & Yoder 2015). Most studies working on climate change consequences use correlative methods in order to evaluate the fundamental niche of a species (Crick 2004; Miles *et al.* 2004; Thuiller *et al.* 2005). This means identifying the relative importance of different climatic variables over a species ecological and biological needs. Once the ecological niche of a species has been assessed, it is possible to predict its current and future distribution area using spatially explicit climatic data, such as the one produced by WorldClim (Fick & Hijmans 2017).

Such approach assumes that current species distributions are only limited by abiotic factors, whereas many biotic factors may play a role in restraining a species to its realized niche (Pearson & Dawson 2003). In our case, adding to the historic (Dewar & Richard 2007) and future (Hannah *et al.* 2008) role of climate, the continuously growing threat from deforestation (Harper *et al.* 2007) has become an important driver shaping the future of Madagascar biodiversity. Over the past centuries, Malagasies forests have been sorely reduced, with less than 15% of the original forest remaining (Harper *et al.* 2007) and deforestation rate steadily increasing (Vieilledent *et al.* 2018). As these forests are known to harbour more than 80% of Madagascar total biodiversity (Waeber *et al.* 2019), their integration into the ecological modelling process of species niches appears important. But if future climatic data are globally available, future forest cover have mostly been produced for the Amazonian forest (Soares-Filho *et al.* 2006). Although, recently, the production of a high resolution future deforestation map (Vieilledent *et al.* in prep.) for Madagascar has enabled the possibility to further investigate the fate of its biodiversity.

In Madagascar, deforestation has already been held accountable for the loss of around 9.1% of terrestrial species from 1950 to 2000 (Allnutt *et al.* 2008). Therefore, we took this new map as an opportunity to explore through a new angle the effect of deforestation and compare it to the threat of climate change. We used an ensemble forecasting approach in order to model the ecological niche on one of Madagascar most iconic taxonomic groups: lemurs. Lemurs are well fitted to investigate both the effect deforestation and climate change; they are highly dependent on forest cover while still able to persist in fragmented landscape (Lehman *et al.* 2006) and are likely to be vulnerable to climate change (Dunham *et al.* 2011). We can expect different responses for species from a same taxonomic group, such as a contraction of the SDA, an expansion outside of its current distribution area or a range shift toward places with newly suitable climate. Such data may yield important information regarding future species

conservation status (Bomhard *et al.* 2005; Coetzee *et al.* 2009). Past studies have used current species distributions map to assess conservation policies in Madagascar (Pearson *et al.* 2007; Kremen *et al.* 2008;), here we explored how future SDA may also be used to identify areas of important conservation value.

In this study we aim to answer these questions: which effect will affect the most the future distribution area of lemurs between climate change and deforestation? How this information can be used to identify areas of conservation? First, we quantified the effects of both climate change and deforestation at the species level and assessed their relative importance. Secondly, by aggregating species results at the community level, we investigated how such information may be used to explore the spatial effect of these different scenarios on lemur's richness. Thirdly, we used this information to determine areas acting as climatic refuges for lemurs and identified the ones threatened by deforestation.

Materials and methods

Statistical analysis were performed within the R environment (R Development Core Team 2008). Geospatial computation were performed within either the GRASS environment (Neteler *et al.* 2012), the R environment or by using the QGIS software (QGIS Development Team 2009).

Species and climate data

Species occurrences

Despite being a well-known taxonomic group, data about lemurs' distributions are relatively scarce. For this reason, we combined information gathered from multiple sources. The main one being the Lemurs Portal and the data gathered and made available by Brown & Yoder (2015). These datasets contain expertly vetted occurrences. The Rebioma database was also added despite it sharing most of its observations with the Lemurs Portal database. Using the 'taxize' package (Chamberlain & Szöcs 2013), observations were checked for deprecated names and taxonomic mistakes against a wide range of taxonomic data sources (*e.g.* IUCN, EOL). Errors were automatically flagged and manually corrected. When species names were deprecated, we updated them to the most recent one according to the literature. Observations were then cleaned using the coordinateCleaner R package (Zizka *et al.* 2019), which allows to automatically flag common spatial and temporal errors (*e.g.* invalid or impossible coordinates, duplicates). Sampling biases, like over prospected areas, were corrected by rarefying the data at a 1km² spatial resolution for every species.

Climatic data

Current and future climatic data were downloaded from the MadaClim website. Madaclim offers a set of 70 variables derived from the WorldClim website (Fick & Hijmans 2017). WorldCilm is a set of global climate layers that were generated through interpolation of average monthly climate data from weather stations tabulated from 1950–2000. Climatic variables for Madagascar were resampled at a 30 arc-seconds resolution and reprojected in the WGS 84/UTM zone 38S projected coordinate system. To the original 19 bioclimatic variables from WorldClim, the MadaClim dataset adds: monthly minimum temperature, monthly maximum temperature, monthly total precipitation, monthly potential evapotranspiration, annual potential evapotranspiration, annual climatic water deficit and the number of dry months in the year. For the analysis, variables were selected after performing a Principal Component Analysis (PCA) on the bioclimatic variables for each cell containing a presence point. In order to select explicit explanatory variable whilst still having as few as possible, we selected four variable that covered most of the variability from the two main axes (41.84% and 35.65%). This left us with annual precipitation (mm), annual temperature (°C x 10), precipitation seasonality (mm) and temperature seasonality (°C x 10). The climatic water deficit was also added to the study for its ability to predict tree distribution (Lutz *et al.* 2010). As correlation between predictor has been identified as an important source of variability (Buisson *et al.* 2010), variables were selected and tested in order to avoid multicollinearity (Braunisch *et al.* 2013).

Climate change scenarios

For future time period (i.e. 2085), we used data from the CCFAS-CGIAR (Ramirez & Jarvis 2008) which consist of prediction, averaged over a 30-year time period (2070-2100). We used prediction from three global circulation models (GCM) under the CMIP5 (IPPC Fifth Assessment): CCSM4, GISS-E2-R and HadGEM2-ES, for two different CO₂ emission scenarios: RCP 4.5 and RCP 8.5. The 4.5 pathway is a stabilization scenario where concentration continues on trend, up until 2070 and then continues to increase, but at a slower rate (Clarke et al. 2007). In this scenario temperatures are expected to increase between 1.1 °C and 2.6 °C. The 8.5 pathway is the business as usual scenario, it's the most pessimistic scenarios where little effort is made to decrease CO₂ emissions (Moss et al. 2008). In this case CO₂ concentrations would increase and reach 950 ppm by 2100 and then continues to increase for another 100 years. Temperatures would rise between 2.6 °C and 4.8 °C. We also added a third scenario where climate would remain exactly as it is today. The three GCM used here were selected for their ability to encompass most of the variability for the two RCP, when compared to other available GCM (Vieilledent et al. 2018). Previously specified variables were computed under each GCM (CCSM4, GISS-E2-R and HadGEM2-ES) and scenarios (4.5, 8.5) for the 2085 time period.

Forest cover and deforestation maps

The forest map for the year 2010 used in this study the was created by Vieilledent *et al.* (2018). The author used a forest map from Harper *et al.* (2007) and completed missing areas with one from Hansen *et al.* (2013) to create a forest cover for the year 2000. This 2000 forest cover map was then combined with the annual tree cover loss maps from Hansen *et al.* (2013) for the years 2001 to 2010. Thus, creating a 30m resolution forest cover map for 2010. For future forest map (year 2085) we used deforestation maps also created by Vielledent *et al.* (in prep.). This map is built from empirical deforestation trends in Madagascar over the last 60 years modelled against a wide range of explanatory variables (distance to the road, distance to

the edge of the forest.), and compensating for variability in deforestation probability between region by adding a spatial random effects. The output are deforestation maps at a 30m resolution for the entire island of Madagascar. We resampled both the current and future 30m forest map to a coarser resolution (30 arc-second, 1km²) using a summing aggregation method and reprojected them into the WGS 84/UTM zone 38S projected coordinate system. This gave us the number of 30m forest cells within a 1km² square. We repeated the aggregation process on a 30m land cover map which gave us the total number of 30m land cell within 1km². From this we were able to compute the percentage of forest cover over land cover per 1km² cell for present and future forest maps. Current variables were rescaled and centred before the analysis. Future variables were rescaled and centred accordingly.

Protected area network

A shapefile representing Madagascar's protected areas (UNEP-WCMC, 2019) was also used in order to compare our results with the already existing network. We used the sf R package (Pebesma 2018) to manipulate these data.

Species distribution modelling

Buisson et al. (2010) showed that SDM choice is one of the main sources of variability in SDMs predictions. As each statistical model works differently to identify the relationship between variables and predictors, it detects independent information with its own errors and uncertainties (Hao et al. 2019). By promoting the use of multiples algorithm, ensemble forecasting aims at "separating more clearly the signal from the noise" (Araujo & New 2007). When dealing with climate forecast, another level of uncertainty, inherent to the nature of these climate forecast, is added. In this case, using multiple GCM allows to produce predictions more consistent with uncertainties in the climate change projections. As RCP scenarios are dependent of international decisions and outcomes can be influenced, we chose to produce maps for each scenario instead of integrating them in the modelling process for each year. Furthermore, as RCP choice has been shown to influence greatly predictions outputs, assessing the different effect of these CO2 pathway on lemur species would allow for a better understanding of their impact. Ensemble models were built for every species that had enough observations point (>10). In total, 5 different ensemble models were projected for each species: one for the current ecological niche and 6 for future alternatives (1 time period x 3 climate assumptions x with/without deforestation). As the no climate change, no deforestation scenario added no information, we reduced this number to 5. Each of these future alternatives were assembled from 15 SDMs (5 statistical algorithm x 3 global climate models). Models were produced with the BIOMOD2 R package (Thuiller *et al.* 2009)

Algorithm choice

We chose 5 widely used statistical models present within the Biomod package: Generalised Linear Models (GLM), Generalised Additive Models (GAM), Maximum Entropy models (MaxEnt), Random Forest (RF) and Artificial Neural Network (ANN). GAMs (Yee & Mitchell 1991) have the advantages to deal with more complex responses curves than GLM, allowing to fit more robust models when dealing with nonlinear relationships (without transformation). MaxEnt (Phillips *et al.* 2006) is a machine learning algorithm for modelling species distributions from presence-only records based around the principle of maximum entropy. It has been extremely used because of its easy to use interface and its robustness to biased samples (Phillips *et al.* 2009; Elith *et al.* 2011). Random Forest is a supervised classification algorithm that creates a collection of decision trees from random samples of rows and predictors. Predictions are made by averaging these trees through 'voting' (Breiman 2001). RF major advantage lies on its ability to avoid overfitting. Finally, ANN is an information processing model that works by adjusting the weights of an internal structure made of multiple inputs (Stergiou 1996).

Algorithm parameters

Statistical models were set as followed: GLMs with linear and quadratic terms, disabling any interaction possibilities. A stepwise procedure, using the AIC criterion (Akaike 1974), was used to select the best model for each species. For GLMs, a minimum of 30 occurrences was required. For GAMs we used cubic spline smoother (s) with a degree of smoothness set to 4 for each variable. For MaxEnt in order to limit overparameterization (Merow *et al.* 2013), product, threshold and hinge were set to false. Which means we only used logistic outputs for our models, making it equivalent to the predictions of GLMs or GAMs (Elith *et al.* 2011). For Random Forest, a regression was computed from 500 hundred trees. For the ANN a 5-fold cross-validation was realised for each species to find the best number of units in the hidden layer (selected between 2, 4, 6 or 8) and the best parameter for weight decay (selected between 0.001, 0.01, 0.05 or 0.1). Other parameters were kept as default.

BIOMOD's modelling options

As we did not have real absences for our species, 10 000 pseudo-absences points were randomly selected to fit our models. For model evaluation we performed a cross validation procedure, randomly splitting the data into 70% in training data and 30% in testing data. For

every statistical models we computed three model evaluation metrics using the testing dataset: the True Skill Statistic (TSS) (Peirce 1884), the Area Under the Curve (AUC) (Mason & Graham 2002) and the Overall Accuracy (OA) (Finley 1884).

Accuracy metrics

The AUC is a threshold independent metric equivalent to the probability that the "model will rank a randomly chosen presence site higher than a randomly chosen absence site" (Liu *et al.* 2011). Prediction accuracy is considered to be excellent when greater than 0.9 (Swets 1988). TSS is a threshold dependant metric (Liu *et al.* 2011) that has the advantage of not being sensitive to prevalence (Allouche *et al.* 2006). TSS is calculated as the sum between sensitivity and specificity minus one. Sensitivity is the proportion of actual positives that are correctly identified, and specificity is the proportion of actual negatives that are correctly identified. OA is a simple measure of model performance widely used in ecology. It's defined as the probability that a positive or a negative is correctly predicted (Liu *et al.* 2011).

Committee averaging

Before combining predictions from individual models into an ensemble model we first transformed individual models' outputs from probabilistic predictions to binary prediction using the TSS optimal value. We then summed binaries predictions from each model, in order to create a voting system, where each cell has a score ranging between 0 and the number of validated SDMs (5 max. for current niche and 15 max. for future alternative). We consider a cell as part of a species ecological niche when at least half (rounded up) of its SDMs predict a presence. SDMs with TSS value lower than 0.5 were excluded from ensemble models.

Data Analysis

Species' dispersal capabilities

As climate continues to change, species are expected to gradually migrate from no longer suitable habitat to one with better conditions. Their ability to colonize such habitat is then highly dependent on their dispersal capabilities. When this information is unknown, the common approach is to consider two extreme scenarios of range change (Thomas *et al.* 2004; Coetzee *et al.* 2009). We considered that species may either: disperse to any given point over the surface of Madagascar (full dispersal scenario) or, constrain to their current niche (zero dispersal scenario). This method has been widely used and we can expect reality to fall somewhere in between those two extremes. Both of this scenario where applied to each of the 5 future ensemble models, effectively doubling our number of future ensemble models (table

1). Under full dispersal, future niche alternatives were kept as predicted but under zero dispersal, future niche were masked using the current one.

#	Dispersal	Deforestation	Climate change
1	Zero	No	4.5
2			8.5
3		Yes	No
4			4.5
5			8.5
6	Full	No	4.5
7			8.5
8		Yes	No
9			4.5
10			8.5

Table 1: Different assumptions combinations used in this study for future ensemble models

Species distribution area change

For every species, we calculated the surface gained and lost under each scenario. This allowed us to estimate the percentage of change in species distribution area (SDA) across all ensemble models and further characterize species response. We defined different classes of species' responses from a Hierarchical Clustering Analysis (HCA) performed with the Ward's criterion on the percentage of changes for the 9 different future ensemble models. Ward's Criterion works by trying to minimize inertia inside a same group while maximizing it between different groups (Ward 1963). The number of classes was selected by graphical interpretation of the output and with the help of Husson et al. (2010) "between-cluster inertia" method. The HCA was realised using the 'ade4' R package (Dray & Dufour 2007). As some species experienced important range change, percentage of changes were log transformed before analysis. A mixed effect linear model was built to better understand the effect of climate and deforestation on SDA change. As we used SDA change from different scenarios for the same species, we added a random effect from these species. The use of a mixed model was validated by comparing AIC values between a classic linear model and a mixed model performed with the lme function from the nlme R package (Pinheiro et al. 2019), under the REML method. The use of a linear model was validated by checking that residuals followed a normal distribution and that the variance of the error terms was constant over the entire feature space. We then use an ANOVAs to isolate the relative importance of climate change and deforestation on the variability of the results. As the lme function didn't permit to perform an ANOVA on model output, we used the lmer function from the lme4 R package (Bates et al. 2015). Mixed model total r-square was computed using the r.squaredGLMM function from the "MuMIn" R package (Barton 2009).

Core range shift

To further characterize the effect of climate change on species, we identified core range shift from current to future SDA. To do so we computed the centroid of every SDA under each scenario. We then computed the vector between current and futures SDA centroids. In order to identify important dispersal areas, we calculated the density of overlapping vectors through every scenario and every species. This was performed by firstly transforming vectors into evenly separated points (each point at 1 km from each other) and secondly, calculating the Kernel Density of points in a 50 km radius, on a 1km grid cell. This gave us areas potentially important for lemurs' dispersion into more suitable habitats. Statistical models were built to better apprehend the effect of climate and deforestation on dispersal distance. We built a mixed effect linear model following the same procedure explained previously.

Identifying areas of high conservation interest

Although the richness of site can be a good measure of its biodiversity value, using only this information will be at the expense of less abundant, range-restricted or isolated species. One way to correct this can be by giving more weight to species with smaller distribution area. Doing so would ensures that it's not only the site with the most species that are selected, but also the one with species underrepresented over the area of interest (i.e. Madagascar). This approach has been applied before when trying to identify new protected areas (Rodrigues et al. 2004) or when prioritizing efforts among existing one (Le Saout et al. 2013) and the resulting attribute is called "irreplaceability". Irreplaceability can be defined as "the potential contribution of a site to a conservation goal by virtue of the features it contains" (Pressey et al. 1994). It is usually calculated over large and geographically limited areas as a mean to identify the ones needing to be protected the most, under specific sets of conservations target (Coetzee et al. 2009; Le Saout et al. 2013). Numerous approaches have been developed to calculate irreplaceability (Carwardine et al. 2007), here we chose to follow Le Saout et al. (2013) method for its easiness to implement. The authors calculate irreplaceability as the sum of species found in an area, weighted by the proportion of each species' range. This means that an area irreplaceability will increase the more species it contains and the smaller these species total distribution areas is. In our case, an area is simply defined as a cell. Thus, we computed irreplaceability under future scenarios of climate change and deforestation, for every grid cell, as follow: $Ir = \sum S_i * \frac{1}{sda}$ where $S_i = 1$ if a species is present in a cell, and equals 0 otherwise, and sda = total species distributional area.

Assessing climate change and deforestation impacts

To evaluate the impacts of climate change and deforestation under each scenario, we computed the number of species gained and lost per grid cell. From this we calculated a species turnover rate (Tr) by applying for every cell the following equation: $Tr = \frac{G+L}{R+G}$ where G is the number of species gained, L the number of species lost and R the current species richness. A value of 0 indicates no change in the species assemblage of a grid cell. A value of 1 indicates an entirely different assemblage from the previous one. Thus, areas with smaller values of turnover indicates a better stability of the species assemblage present on this location. Under zero dispersal scenarios, this turnover rate corresponded to a percentage of species lost, as gain is impossible.

Identifying refuges threatened by deforestation

Irreplaceability and turnover have both been used simultaneously before to define high priority conservation areas, by promoting places presenting both high vulnerability and high irreplaceability (Reyers 2004; Coetzee *et al.* 2009). In order to identify areas capable of maintaining their current community, we followed a similar method by selecting sites with high irreplaceability but low vulnerability. Effectively, this allows us to select places containing both species with a small distribution area or/and with a high richness, whilst also being areas less likely to suffer from climate change. We performed this process, and identified these refuges, across scenarios.

In order to identify areas where deforestation would be the more harmful for lemurs' conservation against climate change, we subtracted areas identified as refuges from no deforestation and deforestation ensemble models. This meant going from ten future ensemble models back to five. This allowed us to recognize high priority conservation areas threatened by deforestation under every scenario of climate change and dispersal. Madagascar's protected areas were then projected over the identified areas in order to compute the amount already protected within the existing protected network. We also calculated the number of species predicted to be present within these areas in the current ensemble model.

Results

Analysis were performed across every scenario but for better visualisation, results are in some cases only shown for the most extreme one (8.5, zero/full dispersal). We chose these scenarios because they better illustrate the processes in action.

Dataset preparation

From the three initial data sets, containing a total of 88 species over 9571 observations, we were left afterward with only 3375 observations, which allowed us to effectively model the ecological niche of 51 species (table 2; see annex I for a more detailed version). As expected, a considerable chunk turned out to be strictly equivalent duplicates (4096 observations) and were deleted. As data were originally expertly vetted, we only found a few species with taxonomic, orthographic, spatial or temporal errors. 215 observations did happen to have their coordinates located above sea, but this might come from the 1km² grid we used, failing to follow Madagascar coastline precisely or the fact that not every island was included in the analysis. The rarefaction process resulted in the removal of 2150 observations. Over this dataset, 49 species (55.6%) are classified as endangered (EN), 19 as critically endangered (CR) and 19 as vulnerable (VU).

	Original Data Sets			Modified Data Sets			
Family	Brown & Yoder, 2015	Lemurs Portal	Rebioma	Aggregated	Aggregated & Checked	Aggregated & Checked & Rarefied	
Cheirogaleidae	570	373	352	1295	800	674	
Daubentoniidae	44	46	46	136	87	79	
Indriidae	991	492	478	1961	1151	893	
Lemuridae	1184	2214	2131	5529	3095	1443	
Lepilemuridae	379	144	127	650	392	286	
Total	3168	3269	3134	9571	5525	3375	

Table 2: Number of observations classified by lemurs' families. Column under "Modified Data Sets" show the same dataset after being aggregated, cleaned and rarefied.

Modelling process

Overall, ensemble models had a good predictive capacity for most species (table 3). AUC values for the full dataset were consistently above 0.968, with a median equal to 0.998. TSS value were slightly lower, with a minimal value at 0.70, which is still considered "useful" (Coetzee *et al.* 2009). Only 5 species had a TSS under 0.8 while 50% of the models showed a good score (>0.922). OA values were also satisfactory with no models falling under 0.8. Consistently with others authors observations (van Proosdij *et al.* 2016), model performance was usually better for species with narrower niche, while species showing the worst score were mostly one with wide geographical range.

Table 3 : Minimum, maximum and median values for three accuracy metrics calculated over the 51 ensembles models constructed. OA = Overall Accuracy, ROC = Receiver Operating Characteristic, TSS = True Statistical Skill

N = 51	Min	Max	Median
AUC	0.969	1	0.999
OA	0.802	0.998	0.929
TSS	0.71	0.998	0.922

Species' responses

Under the most optimistic scenario (RCP 4.5, full dispersal and no deforestation) 59% of all SDA suffered a reduction in range (Annex II). When deforestation was taken into consideration for the same scenario, the percentage of ensemble models showing a smaller SDA in the future increased to 80.4%. The 8.5 pathway consistently multiplied the number of extinctions from 2 to 5 times more than 4.5 ensemble models, while other categories slightly decreased. Finally, as zero dispersal scenarios prevented expansion, every species experienced a contraction of their habitat under this scenario, to a different extent for each species. For species that would have expended under full dispersal scenarios, this mostly resulted in a small contraction of their niche.

Under the combined effect of climate change and deforestation, four main classes of responses were identified from the HCA using the "between-cluster inertia" method (fig. 1b). A fifth one was added because the underlying processes explaining it were easily identifiable. Classes were built with log transformed data to reduce outliers' weights but interpretation from the HCA output are made on the original values. According to our models, 19 species are predicted to experience a drastic reduction of their habitat (fig. 1a). These species are divided into two classes: the first one corresponds to 8 species showing near extinction across most scenarios with -90.16% $\pm 13.75\%$ mean decrease in SDA, the second one contains the remaining 11 species, which show complete extinction in almost all scenarios with -98.92% $\pm 3\%$ mean decrease in SDA. The third class contains 11 species that are predicted to suffer moderately

from both climate change and deforestation (-60.93% $\pm 26.97\%$). The two remaining classes were mostly defined by the full dispersions' scenarios. Thus, under full dispersion, 9 species are predicted to experience habitat loss due to deforestation (-66.44% $\pm 44.64\%$) while habitat suitability mostly increased with climate change (+38.89 $\pm 78.39\%$). Under full dispersion again, 12 species saw their habitat increase with climate change overwhelmingly compensating the negative effect of deforestation (+148.79% $\pm 199.49\%$). Overall, deforestation decreased SDA by -56.4% ± 1.08 (*p*<0.001), RCP 4.5 decreased SDA by -66.4% ± 1.1 (*p*<0.001) and RCP 8.5 by -80.5% ± 1.1 (*p*<0.001). R-squared value was 62,3% with 19.79% explained by the variables, 14.6% of the total deviance was explained by climate change and 5.2%% by deforestation (table 4).



Figure 1: (a) Lemurs species classified from their response to climate change and deforestation resulting from a hierarchical cluster analysis performed for every species, across every scenario. The 5 resulting classes correspond to 5 type of responses: red = complete extinction, kaki = near extinction, cyan =deforestation induced reduction but climate change induced increase of the habitat, blue=overall increase, purple = important reduction in SDA. The blue dotted lines depict the cut chosen with the "between-cluster inertia" method. The red dotted line shows the actual chosen cut height. (b) Relative percentage of inertia gained from each class, the red dot represents the ideal number of classes when following the "between-cluster inertia" method, the blue dot represents the number of classes chosen

Through every scenario species mostly experience a North-Sud range shift (fig. 2b). More specifically, species mainly followed the North-East direction. The line density analysis (fig. 2a) reveals that most range shift occurs around the Ankeniheny-Zahamena Corridor (CAZ), in most cases, species are predicted to flee the area, following either a northern or southern direction. Extending from the CAZ, most of the eastern rainforest appears as an area supporting an important amount of range shift. A small amount of range shift appeared to cross the central part of the island, showing a change in habitat suitability following the longitudinal axis. RCP 8.5 induced a range shift distances of 101.7km ± 0.19 km (p<0.001). When deforestation was considered, range shifts distances from current to future SDA was 53.2km ± 0.06 km (p<0.001). RCP 4.5 was 56.38km ± 0.19 km (p<0.001). R-squared value was 42,36% with 13.61% explained by the variables, 9.77% of the total deviance was explained by climate change and 3.8% by deforestation (table 4).



Figure 2 : Main areas of species range shift from current to future SDA. (a) A line density analysis map made from every species, across every scenario, highlighting areas of important range shift. (b) Map of core range shift from the centroids of current Species Distribution Areas (SDA) to the ones of future SDA. Each line corresponds to a species with the arrow pointing at the center of the future SDA. Arrows are projected above a map of Madagascar's' forest cover from Vieilledent et al. (2018). Only the ranges shift from the 8.5, full dispersal, with deforestation, ensemble model are projected on this map.

		Char	nge in SDA	A (%)	Range shift (km ²)			
Variables	coef	SE	p value	Deviance explained (%)	coef	SE	p value	Deviance explained (%)
RCP 4.5	-66.4	1.1	<0.001	14.6	56.38	0.19	<0.001	9 77
RCP 8.5	-80.5	1.1	<0.001	14.0	101.71	0.21	<0.001	5.77
Deforestation	-56.4	1.08	<0.001	5.2	53.16	0.06	<0.001	3.8

Table 4: Mixed models outputs (coef = coefficient, SE = standard error) obtained from modelling the effect of climate change and deforestation on SDA relative change and distance between current and future SDA

Community response

Nine species richness maps were produced in total (fig. 3; see annex IV for a bigger version). For the current time period the highest value for species richness are found in the eastern part of Madagascar, around the Ankeniheny-Zahamena Corridor with up to 22 species over one grid cell. Most of the species are present in dense forest areas, mostly on the eastern coast, whereas lowest richness values are more concentrated in the most southern part of Madagascar.



Figure 3: Predicted species richness map from both current (right panel) and futures (left panel) ensemble models $(n \le 51)$.

Future richness distribution patterns remained similar to the current distribution one, with the exception of some regions experiencing heavier contraction. For instance, deforestation models resulted in important contraction toward the few remaining forest habitats. For RCPs, patterns were consistent across scenarios, but species lost increased with stronger carbon emission scenario, especially in areas with high richness (Annex IV). This effect inflated with deforestation. Since some species gained from climate change, full dispersal richness maps were less negatively impacted that zero dispersal one. Species gain mostly occurred in low altitude areas, with places even being newly colonized (fig 4a). Some areas were more impacted than other: under the no deforestation scenarios, the Zahamena national park and the Akeniheny-Zahamenathe corridor suffered the highest species loss across all the island, with richness dropping from 17 species to 0 in multiple scenario (full/zero dispersal, with/without deforestation, 8.5) (fig. 4b, see Annex V for a closer look). Overall, while future richness patterns remained close to current one, species richness mostly decreased at the local scale, regardless of the ensemble model scenario.



Figure 4: Predicted number of species gained (a) and lost (b) under the 8.5, full dispersal, no deforestation scenario

At a larger scale, total species richness dropped from 51 to 34 in the worst case scenario (zero dispersal, deforestation, 8.5) (table 5). Deforestation only scenario were the less impacted, with species richness maintened at their current level. RCP scenarios were consistent, with higher RCP experiencing stronger species loss. As expected, losses were higher when both deforestation and climate change were happening. Mean percentage of habitat lost per species

was negative under all scenario except the 8.5, full dipersal, no deforestation scenario. This particular one is charactherized by species experiencing especially high range expansion. For instance, *Eulemur cinereiceps* distribution area increased by 860%. The same pattern happens for every full dispersal scenario, with each of them experiencing lower habitat loss than their zero dispersal counterpart.

Scenarios			Predictions	
Dispersal	Deforestation	Climate change	Mean percentage and 95% CI of change in habitat surface	Total Richness
Zero	No	4.5	-46.51 (-56.5936.43)	47
		8.5	-60.12 (-70.2250.02)	38
	Yes	No	-52.84 (-58.8146.88)	51
		4.5	-73.69 (-81.4865.89)	44
		8.5	-76.71 (-85.268.21)	34
Full	No	4.5	-0.25 (-40.41-+39.9)	48
		8.5	+14.02 (-33.58-+61.62)	39
	Yes	No	-52.84 (-58.8146.88)	51
		4.5	-43.88 (-70.3417.43)	44
		8.5	-23.75 (-59.75-12.26)	37

Table 5: Predicted percentage of habitat lost (Mean and 95% confidence interval (CI)) and total richness across every species and under each scenario.

Identifying refuges

We identified refuges as places with both high conservation value, *i.e.* high irreplaceability, and low vulnerability, *i.e.* low turnover. We considered areas with a turnover inferior to 50% as "climatically stable", meaning that we only selected places capable of holding more than 50% of their current assemblage. To select high conservation values areas, we chose to only keep the top 10% most irreplaceable areas.

Species turnover assessment were mostly similar between every scenario, with some minor differences depending on the initial conditions. For dispersal capability, the difference laid in species ability to colonize new areas, effectively increasing the turnover of this places. Accounting for deforestation resulted in an almost 100% turnover rate over deforested areas, while other places stayed in line with climate only models. Different RCPs outputs were consistent with each other and presented similar spatial pattern of species turnover. The only differences being that species turnover was higher with stronger CO2 emissions scenarios. Globally, high altitude areas and the northern part of the island experienced a strong turnover

(>60%). Places already identified for their important loss in richness (Zahamena national park and the Akeniheny-Zahamenathe corridor) experienced an important turnover rate as well.

As expected, irreplaceability increased with the number of species while still accounting for areas with lower richness but species with narrower niches (fig. 5a). Even though through every scenario, the eastern humid forest appeared as highly irreplaceable, other areas were highlighted as well. For instance, the western coast consistently had patches of habitat identified as highly irreplaceable. The northern part of the island, despite experiencing some of the strongest turnover rate, also presented places of high conservation values. Although, most of these areas considerably contracted, or even disappeared, when switching from RCP 4.5 to 8.5.



Figure 5: (a) Smoothed color density plot obtained by plotting future irreplaceability against species richness. (b) Future irreplaceability plotted against species turnover. Grid cells with low turnover (<0.5) and high irreplaceability (top 10%) are considered important for lemurs' conservation. Both figures have been produced under the 8.5, zero dispersal, no deforestation scenario.

Selecting only the most climatically stable places (turnover <0.5) meant that the total area identified as refuges dropped under the 10% irreplaceability threshold, down from 9.7% to only 3% of lemurs' total distributional area. This indicates that despite being highly irreplaceable in the future, some places were not selected as they had already experienced strong turnover over the considered time period (fig. 5b). We obtained 10 maps of lemur's refuges, one for each combination. Across every ensemble, the selected areas were mainly inside the already protected area network, with it covering at least 56% of the cell identified as refuges, and up to 75% (table 6).

	Scenari	OS	Refuges						
Dispersal	Climate change	Deforestation	Total Area (km²)	Proportion of lemurs' current habitat covered (%)	Number of species covered	Proportion within the protected area network (%)	Proportion threatened by deforestation (%)		
Zero	4.5	Yes	19852	5.1	50	68.8	60		
	4.5	No	29962	7.7	51	63.4	09		
	8.5	Yes	15516	4	50	68.5	60.4		
	8.5	No	27674	7.1	50	65.9	69.4		
	No	Yes	27809	7.1	51	65.5	/		
Full	4.5	Yes	19110	4.9	50	69.3	70.4		
	4.5	No	37252	9.5	51	62	/0.4		
	8.5	Yes	11542	3	46	72	72 5		
	8.5	No	27690	7.1	51	61	75.5		
	No	Yes	26546	6.8	51	59	/		

Table 6: Refuges characteristics under each scenario before and after being aggregated pair wise

Finally, we subtracted corresponding combination of scenario made with and without deforestation, reducing the total number of refuges maps to five. This gave refuges maintained with and without deforestation, and the one threatened by deforestation (fig. 6a). Across our final five maps, at least between 69% and 73.5% (table 6b) of areas identified as refuges were threatened by deforestation.



Figure 6: (a) Areas identified as refuges under zero dispersal, 8.5, no deforestation model climate b) Refuges maintained despite deforestation (green) and threatened by deforestation (red)

Discussion

Climate change and deforestation effect on lemurs

Out of the 51 species studied in this analysis, 30 are predicted to undergo important distribution contraction in the future (fig. 1). Other species are only predicted to increase their current distribution area under a full dispersal scenario and would otherwise still lose some of their climatically suitable spaces. Our models predict that climate change only will be responsible for the range contraction of 58.8% (30 out of 51) of lemurs' species considered in this study. This number increased to 74.5% (38 out of 50) when considering both the effect of climate change and deforestation. Previous study on lemurs also found important range reduction for 62% of the species considered (Brown & Yoder 2015). Our results are relatively comparable even though we used the forest cover as well as climatic data (previously cited study only worked with climate), both an updated and a stronger carbon emission scenario, species with at least 10 observation (against six) and didn't filter species based on the size of their niche. As of 2019, the IUCN Red List (IUCN 2019) consider 95% of lemurs species as threatened. Thus, the consequences of the threat identified in this study would be considerable for a taxonomic group already suffering from" important pressure. This result emphasizes once again the need for IUCN Red List to adapt their methodology in order to acknowledge the effect of climate change (Bomhard et al. 2005; Coetzee et al. 2009). Currently, the time scale used to assess the status of a species isn't long enough to consider the harmful effect of slow processes like climate change (IUCN, 2019), but this could change in the future (Foden & B.E. Young 2016).

Our prediction indicates that species range are most likely to shift northward and southward (fig. 2a), especially along the humid forest of the eastern coast, where most species may be encountered (fig. 3). Once again, our results here corroborate with the one previously shown by Brown & Yoder (2015) and only help emphasize on the importance to conserve this areas. Such forest may act as corridors (Hannah *et al.* 2008) and conservation regarding these areas seem indispensable in order to support the important change in SDA previously mentioned. As the area supporting the densest range shift happen to be already importantly deforested (fig. 2b), conservation polices there would be inadequate and restoration efforts should be investigated. At a smaller scale, many other places may need restoration to support future migration. As expressed by Hannah *et al.* (2008), riverine corridor are important pathway for species migration, but the same rivers can also be seen used in Madagascar as a mean for human to expand further into forested areas. Such places would require important conservation

effort to support future species range shift. Unfortunately, the scale of our study doesn't allow us to identify these places and doing so would require further investigation.

Rivers may also act as barrier and prevent any dispersal opportunities (Pastorini *et al.* 2003). Accounting for these barriers in the modelling process can be achieved but doing so would have important consequences on modelling outputs (Nakazawa 2013). But still, as it doesn't account for any kind of limitation, our full dispersal scenarios may be overestimating species distributions areas. For this reason, scenarios from the zero dispersal assumption may be closer to reality. Despite this, our models can still be considered relatively conservative regarding the future of lemurs for several reason: deforestation rate are calculated from an historical mean and do not account for demographic growth; climate change is currently on trend with the 4.5 scenario; some lemurs have exigence regarding forest quality (Ganzhorn 1989) and we didn't account for the effect of forest degradation .

Disentangling the role of climate change and deforestation

Climate change and deforestation effects on SDA were relatively similar (table 4). Both resulted in a mean SDA contraction of more than half its original size over the next 75 years. But looking at the explained deviance, climate change caused an almost three times higher deviance in the change of suitable habitats than deforestation did. Meaning that climate change had a relatively more important role in predicting the future of a species distribution area than deforestation. The same observation can be made regarding range shift distance between current and future SDA, with the explained deviance ratio between climate change and deforestation being almost identical to the SDA change one. Using a similar approach but analysing only the percentage of habitat loss, Feeley *et al.* (2012) observed similar patterns within the Amazonian forest. In our case, the observed difference in the explained deviance between these two assumptions may come from different sources:

One reason might be that despite being recognized as highly reliant on the presence of a forest cover, some lemurs species are known to survive in more fragmented habitats (Lehman *et al.* 2006) or even agroforestry system (Faranky Ravelomandrato, personal communication, July 31, 2019). Ensemble models built from species occurrences observed in such areas would account for the relative resistance of these species against deforestation. Thus, when predicting the impact of deforestation, these species would be expected to be less negatively impacted than others. Another reason explaining climate change strong effect on SDA change come from the observation that no species disappeared under deforestation only models (table 5). On the

opposite, climate change best case scenario led to the extinction of three species. Further investigations need to be realised in order to further characterize the way climate change impact lemurs SDA. But preliminary results indicate that species with small distribution areas (< 20 000 km²) and located either in the north or the south of the island had their distribution area shrink more importantly than other species. This was the case for every species predicted to go extinct in our hierarchical cluster analysis (fig 1, red group). For each of them, climate change greatly reduced SDA while deforestation effect wasn't as important. Two reasons may explain this: first, the most northern and southern part of Madagascar are expected to experience important climatic change regarding seasonality (Hannah *et al.* 2008; Tadross *et al.* 2008). Secondly, species with small distribution areas usually also have narrow niche. Thus, as species with small distribution are known to be greatly affected by environment change (Murray *et al.* 2011), the role of climate change may appear predominant for these species.

Overall, deforestation effect is consistent across every scenario (table 5). Even if the intensity of the response varies between lemurs' species, forest loss effect is relatively direct and always in the same direction. On the opposite, climate change impact on species distribution area can be both beneficial or damaging (fig. 1b, table 5). With, in some cases, climate change positive effect on some SDA overcoming the negative effects of deforestation. Such variability in species response may explain why SDA change was mostly explained by climate change. Other studies have observed extremely different responses from climate change for species closely related (Vieilledent *et al.* 2013; Brown & Yoder 2015). This emphasize the fact that future lemurs will be highly dependent on their ability to tolerate, or adapt, to important change in both temperature and precipitation regimes. The capacity of these species to endure those changes is one the most important sources of uncertainty regarding the fate of tropical biodiversity (Feeley *et al.* 2012). These results imply that lemur's conservation should mostly focus on preserving from deforestation areas that will remain climatically stable in the future, *i.e.* refuges.

Conservation implications

Both irreplaceability and turnover have been used before to measure conservation importance (Margules & Pressey 2000; Reyers 2004) and their use as a mean to identify climatic refuges has been evoked (Coetzee *et al.* 2009). But to our knowledge, no studies attempted to use it, which may be due to the limits of these indices. Irreplaceability strength lays in its ability to class areas by the relative contribution of the feature existing inside them (Pressey *et al.* 1994). This ability also means that if several species distributed over narrow

niches happen to be in the same place, then this area will have a high irreplaceability value. Such behaviour denotes the important effect of SDM outputs on irreplaceability value. For instance, if a species distribution area is overestimated, which is often the case in Madagascar, then its irreplaceability will drop below its actual value. But, if an irreplaceability value doesn't hold substantial information, its relative importance within the area of interest may still be potentially useful in determining areas of high conservation values under future climatic conditions (Coetzee et al. 2009). In addition, we argue that building better models by using more than just climatic variable, as we did with forest cover, helps reduce overpredicting SDA. Species turnover also might be subject to some limitations. For example, beta diversity indices are known to overemphasize the role of rare species, as the difference in species composition between two areas, between space or in our case time, will reflect the presence or absence of these rare species (Baselga 2010). Also, because of the way we calculated our turnover, we penalized areas for acquiring new species. Although, this only affected full dispersal scenario, which, considering the several difficulties for lemurs to disperse over Madagascar (Hannah et al. 2008; Brown & Yoder 2015), might not be the most appropriated scenario to identify areas of climatic refuges. But, when considering species with important dispersal capabilities, such as birds, then using a different equation might be justified.

While our approach may suffer from some limitations, we managed to identify areas with high conservation values in the future (fig. 5a). Although most of these areas were already the one less impacted by climate change (fig 5b), removing areas with a species turnover superior to 0.5 did reduce the number of places identified as refuges. At least half of the places we identified as refuges happened to already be a protected area. This is mainly because Madagascar protected area network have been designed around remaining forest habitats (Gardner et al. 2018). As lemurs are mostly found in forest, these protected areas are relatively well suited for their conservation. But in order to be efficient, conservation policies should consider species from as many taxonomic groups as possible and across different habitats (Kremen et al. 2008) Nevertheless, these results are promising but denotes that effort still need to be made in order to fill the important gaps that remain in the current protected area network. Especially along the eastern coast, where protected forests suffer from important discontinuity between them (fig 6a). In order to both protect climatic refuges and important migration corridor, conservation effort there need to be developed. This particularly true for areas identified as threatened by deforestation (fig. 6b). The fact that more around 70% of areas identified as refuges would disappear due to deforestation is alarming. Primarily because the deforestation model used here is fairly conservative, as it doesn't account for demographic growth (Vieilledent *et al.* in prep.), and that actual deforestation could be worst.

Conclusion

The use of ensemble modelling in this study helped to account for inter modal uncertainty and produced more accurate projections. It allowed us to explore multiples scenarios and assess their effect on biodiversity. Although the presented predictions describe a wide range of possible outcome of climate change and deforestation, more permutation are still possible. For instance, we only used one deforestation map. Future study should explore multiples forest loss scenarios.

The main results emerging from this study is that if lemurs can't adapt their niche to tolerate climate change, then its negative effect is predicted to have more impact than the effect of deforestation. Such results reaffirm the need for international effort in order to reduce carbon global emission. Although, these results don't imply that deforestation is harmless for lemurs. We propose that conservation policies regarding deforestation consider protecting in priority areas that will facilitate biological responses to climate change.

We identified such areas by exploring the use of irreplaceability and species turnover as mean to quantify the effect of climate change. More work still needs be done in order to explore and refine methods to prioritize conservation policies regarding climate. We reiterate that future study should consider working with a wide range of taxonomic groups from different habitats.

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Annexes:

Annex I: Number of observations for each lemur species. Column under "Modified Data Sets" show the same dataset after being aggregated, cleaned and rarefied.

		Ori	ginal Data	Sets	Modified Data Sets		
Family	Species	Brown & Yoder, 2015	Lemurs Portal	Rebioma	Aggregated	Aggregated & Checked	Aggregated & Checked & Rarefied
Cheirogaleidae	Allocebus trichotis	0	8	8	16	8	8
Indriidae	Avahi betsileo	11	0	0	11	4	4
Indriidae	Avahi cleesei	5	0	0	5	2	1
Indriidae	Avahi laniger	75	107	105	287	164	126
Indriidae	Avahi meridionalis	10	7	9	26	15	9
Indriidae	Avahi mooreorum	10	0	0	10	10	1
Indriidae	Avahi occidentalis	25	10	5	40	24	18
Indriidae	Avahi peyrierasi	27	8	8	43	25	10
Indriidae	Avahi unicolor	8	3	3	14	8	8
Cheirogaleidae	Cheirogaleus crossleyi	3	9	9	21	12	12
Cheirogaleidae	Cheirogaleus major	48	130	125	303	168	123
Cheirogaleidae	Cheirogaleus medius	44	36	29	109	65	62
Cheirogaleidae	Cheirogaleus ravus	2	0	0	2	2	2
Daubentoniidae	Daubentonia madagascariensis	44	46	46	136	87	79
Lemuridae	Eulemur albifrons	47	20	17	84	71	58
Lemuridae	Eulemur cinereiceps	81	2	2	85	33	30
Lemuridae	Eulemur collaris	120	20	19	159	93	64
Lemuridae	Eulemur coronatus	27	5	3	35	27	26
Lemuridae	Eulemur flavifrons	52	0	0	52	15	15
Lemuridae	Eulemur fulvus	114	258	240	612	335	232
Lemuridae	Eulemur macaco	59	3	3	65	35	33
Lemuridae	Eulemur mongoz	6	11	5	22	9	9
Lemuridae	Eulemur rubriventer	47	75	63	185	113	98
Lemuridae	Eulemur rufifrons	110	3	3	116	115	111
Lemuridae	Eulemur rufus	39	28	12	79	55	53
Lemuridae	Eulemur sanfordi	19	1	0	20	20	20
Lemuridae	Hapalemur alaotrensis	0	0	5	5	5	5
Lemuridae	Hapalemur aureus	34	27	23	84	61	46
Lemuridae	Hapalemur griseus	62	286	278	626	343	197
Lemuridae	Hapalemur meridionalis	9	10	10	29	18	13
Lemuridae	Hapalemur occidentalis	9	34	34	77	43	32
Indriidae	Indri indri	219	187	165	571	287	173
Lemuridae	Lemur catta	151	28	22	201	151	132
Lepilemuridae	Lepilemur aeeclis	11	0	0	11	6	5
Lepilemuridae	Lepilemur ahmansonorum	8	0	0	8	5	4
Lepilemuridae	Lepilemur ankaranensis	52	0	0	52	40	24
Lepilemuridae	Lepilemur betsileo	6	0	0	6	5	
Lepilemuridae	Lepilemur dorsalis	19	5	4	28	22	18
Lepilemuridae	Lepilemur edwardsi	55	12	5		39	27
piioinuiiuue		55	14	5	12	57	27

Lepilemuridae	Lepilemur fleuretae	1	0	0	1	1	1
Lepilemuridae	Lepilemur grewcockorum	4	0	0	4	3	2
Lepilemuridae	Lepilemur hubbardorum	17	0	0	17	14	8
Lepilemuridae	Lepilemur jamesorum	10	0	0	10	1	1
Lepilemuridae	Lepilemur leucopus	26	1	1	28	25	13
Lepilemuridae	Lepilemur microdon	19	8	8	35	16	15
Lepilemuridae	Lepilemur milanoii	15	0	0	15	12	4
Lepilemuridae	Lepilemur mittermeieri	1	0	0	1	1	1
Lepilemuridae	Lepilemur mustelinus	40	94	88	222	118	84
Lepilemuridae	Lepilemur petteri	5	4	4	13	7	6
Lepilemuridae	Lepilemur randrianasoloi	20	0	0	20	9	9
Lepilemuridae	Lepilemur ruficaudatus	6	13	13	32	16	16
Lepilemuridae	Lepilemur sahamalazensis	6	1	1	8	2	4
Lepilemuridae	Lepilemur seali	31	0	0	31	29	25
Lepilemuridae	Lepilemur septentrionalis	10	6	3	19	10	7
Lepilemuridae	Lepilemur tymerlachsoni	10	0	0	10	5	1
Lepilemuridae	Lepilemur wrightae	7	0	0	7	6	6
Cheirogaleidae	Microcebus arnholdi	10	0	0	10	9	6
Cheirogaleidae	Microcebus berthae	2	2	2	6	4	4
Cheirogaleidae	Microcebus bongolavensis	3	0	0	3	3	3
Cheirogaleidae	Microcebus danfossi	8	0	0	8	7	8
Cheirogaleidae	Microcebus griseorufus	30	17	20	67	48	41
Cheirogaleidae	Microcebus jollyae	6	0	0	6	4	3
Cheirogaleidae	Microcebus lehilahytsara	2	10	10	22	11	10
Cheirogaleidae	Microcebus mamiratra	1	0	0	1	1	1
Cheirogaleidae	Microcebus margotmarshae	5	0	0	5	4	3
Cheirogaleidae	Microcebus mittermeieri	2	0	0	2	2	2
Cheirogaleidae	Microcebus murinus	112	41	38	191	118	100
Cheirogaleidae	Microcebus myoxinus	8	6	6	20	12	12
Cheirogaleidae	Microcebus ravelobensis	28	4	4	36	30	26
Cheirogaleidae	Microcebus rufus	150	78	73	301	177	148
Cheirogaleidae	Microcebus sambiranensis	16	1	1	18	18	15
Cheirogaleidae	Microcebus simmonsi	6	0	0	6	5	4
Cheirogaleidae	Microcebus tavaratra	44	0	0	44	30	18
Cheirogaleidae	Mirza coquereli	13	9	10	32	21	22
Cheirogaleidae	Mirza zaza	8	1	1	10	6	9
Cheirogaleidae	Phaner furcifer	19	15	10	44	29	26
Cheirogaleidae	Phaner pallescens	0	6	6	12	6	6
Lemuridae	Prolemur simus	59	1251	1246	2556	1295	95
Indriidae	Propithecus candidus	16	3	3	22	20	18
Indriidae	Propithecus coquereli	85	9	6	100	52	36
Indriidae	Propithecus coronatus	22	37	36	95	53	44
Indriidae	Propithecus deckenii	125	31	29	185	93	90
Indriidae	Propithecus diadema	35	52	69	156	108	93
Indriidae	Propithecus edwardsi	119	9	2	130	62	54
Indriidae	Propithecus perrieri	8	0	0	8	8	8
Indriidae	Propithecus tattersalli	46	4	3	53	37	37
Indriidae	Propithecus verreauxi	145	25	35	205	179	163
Lemuridae	Varecia rubra	43	11	5	59	31	23
Lemuridae	Varecia variegata	96	141	141	378	227	151

Scenarios			Predicted Impact on Species Distribution Area				
Dispersal	Deforestation	Climate change	Complete extinction	Contraction >90%	Contraction <90% & >50%	Contraction <50% & >0%	Expansion >0%
Zero	No	4.5	2	10	9	30	-
		8.5	11	8	10	22	-
	Yes	No	0	0	28	23	-
		4.5	5	11	25	10	-
		8.5	14	9	19	9	-
Full	No	4.5	1	9	9	11	21
		8.5	10	5	12	5	19
	Yes	No	0	0	28	23	0
		4.5	4	12	20	5	10
		8.5	11	11	14	2	13

Annex II: Predicted impact on SDA for every scenario combination under five classes of responses

Annex III: Cumulative histogram of species lost across every ensemble models. Dispersal scenario aren't represented as species lost may only occur upon areas already colonized









Annex V: Predicted number of species lost under the 8.5, full dispersal, no deforestation scenario

Abstract

Madagascar is recognized for its high level of endemism. This exceptional biodiversity has been increasingly threatened by both climate change and deforestation. In this study, we estimated the relative importance of climate change and deforestation in predicting the future distributions areas of 51 species of lemurs and identified their climatic refuges. We used an ensemble modelling approach with five species distributions model (GLM, GAM, MAXENT, RF & ANN). We projected species distribution in 2085 using an ensemble forecasting approach and five general circulation models. We assessed the importance of climate change and deforestation by performing a linear analysis on the percentage of change between current and future species distribution areas. An irreplaceability and a species turnover analysis were used to highlight refuges. Climate change appeared as the main driver of species distribution areas. We argue that conservation policies regarding deforestation should prioritize the conservation of climatically stable areas.

Keywords: Bioclimatic niche modelling, lemurs, climate change, deforestation, conservation

Résumé

Madagascar est reconnue pour son fort taux d'endémisme. Cette biodiversité est soumise aux contraintes du changement climatique et de la déforestation. Ici, nous estimons la part relative de ces contraintes dans la prédiction du changement d'aire de distribution de 51 espèces de lémuriens et dans l'identification de leurs zones de refuges. Nous utilisons un modèle d'ensemble construit à partir de cinq modèles de niche. Les aires de distribution futures ont été réalisées à partir d'une approche de projection d'ensemble utilisant trois modèles de circulation générale. Une analyse linéaire sur les pourcentages de changement a été utilisée pour comparer les effets du changement climatique et de la déforestation. Une analyse de l'irremplacabilité et du turnover a été réalisée pour identifier les zones de refuges. Le changement climatique apparait comme le principal effet régissant la distribution future des espèces. Nous concluons que les politique de conservation concernant la déforestation devrait se concentrer sur des zones de refuges climatiques.

Mots clefs: Modélisation de niche, lémuriens, changement climatique, déforestation, conservation