



Habitat suitability modelling and environmental drivers of Malagasy fruit bats (Pteropodidae)

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Abstract

Ecological niche models depict suitable areas of habitat for species, as well as the environmental factors that influence them. They provide insights into species demography, ecology and biogeography, which is important information for the conservation of their populations. In this study, ecological niche modelling was used to investigate the habitat availability and conservation status of three threatened fruit bat species (family Pteropodidae) endemic to Madagascar: *Pteropus rufus*, *Eidolon dupreanum* and *Rousettus madagascariensis*. Model construction was done in MaxEnt using climatic and eco-geographical variables. All ecological niche models performed well, although the limited sample size of occurrence points of *E. dupreanum* allowed less accurate delineation of its suitable area. The suitable habitat area was modelled using a 10th percentile training presence threshold and then filtered for forest area, which was only a mean of 21.1% the overall habitat area for all species. As fruit bats roost in trees and caves surrounded by forest, only the forest area within the ecological niche models represents a suitable habitat and has a size ranging 40,647–54,636 km² between species. Results also show that temperature annual range, annual precipitation, and forest cover may be the most important determinants of the occurrence of Pteropodidae. This study identified suitable forest tracts for the three endemic Pteropodids and thus the potential to expand the forest area under protection. It can be useful for further fieldwork to sample more occurrence points, estimating the population sizes of the species within Madagascar, gaining further information about their ecology, and thus facilitating applied conservation efforts of their wild populations.

Keywords Habitat suitability · Madagascar · MaxEnt · Protected areas · Pteropodidae · Species distribution models

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Introduction

The environmental conditions under which populations of different organisms can survive is known as the ecological niche (Hutchinson 1957). The process of analysing ecological niches is ecological niche modelling and it can provide insights into the taxonomy, evolution, demography and biogeography of an organism, and how similar these characteristics are among closely related species (Elith et al. 2006; Sattler et al. 2007; Cabral and Kreft 2012; Hending 2021). It is also a useful technique for assessing how well threatened species are protected in their natural habitat (e.g. Thorn et al. 2009; Ferrer-Sánchez and Rodríguez-Estrella 2016; Grimshaw et al. 2021; Hending et al. 2023a) and how vulnerable they are to ongoing anthropogenic threats and pressures (Thorn et al. 2009; Gonçalves et al. 2021). Ecological niche models (ENMs) provide a basis for assessing the likely distribution of populations under current and future climate trajectories (e.g., Morovati et al. 2020; Raman et al. 2020; Bandara et al. 2022; Fialas et al. 2025). They are also particularly useful for species whose geographic distributions have been historically understudied (Picot et al. 2007; Aguiar et al. 2020) or are rare and difficult to find in their natural environment (Caruso et al. 2015; Schüßler et al. 2023). As ENMs can be created with little range data (Elith et al. 2006; Pearson et al. 2007; van Proosdij et al. 2016), it is a very useful method if the presence or absence of a species is difficult to be confirmed at a specific location (MacKenzie et al. 2005; Black 2020; Garbino et al. 2023), and ENMs have successfully been used to model the distributions and geographic ranges of cryptic taxa (e.g., Sattler et al. 2007; Santos et al. 2014; Hending 2025).

Madagascar is the fourth largest island in the world and is home to an impressive diversity of species in terms of evolutionary history (Ganzhorn et al. 2014; Antonelli et al. 2022). The different geocological formations and climatic regions of the island provide a variety of habitats and many zones of micro-endemism, which has resulted from the island's long isolation from any other land masses for approximately 88 million years (Wilmé et al. 2006). Furthermore, the island is a biodiversity hotspot and conservation priority due to ongoing deforestation and habitat loss (Harper et al. 2007; Allnutt et al. 2008; Vieilledent et al. 2018). Madagascar has many understudied animals, and ENMs have been successfully used to study their distribution and conservation status (Blair et al. 2013; Boria et al. 2017; Hending et al. 2023a).

This study focuses on three endemic Malagasy fruit bats, *Pteropus rufus* (Madagascan Flying Fox), *Eidolon dupreanum* (Madagascan Fruit Bat) and *Rousettus madagascariensis* (Madagascan Rousette) (Wilson and Mittermeier 2019). They are widespread throughout Madagascar and have been observed inhabiting a range of habitats including forests, mangroves, and agroecosystems (Randrianandrianina et al. 2006; Racey et al. 2009; Hending et al. 2023b), but there are areas where each species is not present (e.g., central highlands for *P. rufus*, far south west for *R. madagascariensis*). While *P. rufus* only roosts in forests, *E. dupreanum* and *R. madagascariensis* also roost in caves (Wilson and Mittermeier 2019). These species provide important ecosystem services and are known to require an availability of trees, for which they are important pollinators and seed dispersers (Aziz et al. 2021; Hending et al. 2021a). This seed dispersal contributes to natural forest regeneration (Wunderle 1997), influences the amount of carbon sequestration and climate change mitigation (Tabarelli and Peres 2002; Estrada-Villegas et al. 2023), and their pollination services are of high economic value for food production (Abrol 2012; Potts et al. 2016; Bello et al. 2021).

For example, *E. dupreanum* feeds on the nectar of baobabs, *Adansonia* spp., and plays an important role in the life-cycle of this culturally important tree (Andriafidison et al. 2006; Raveloson et al. 2014).

The effects of Madagascar's high deforestation rate (Harper et al. 2007; Vieilledent et al. 2018) on the available habitat area for Pteropodids are little studied (Racey et al. 2009). All three endemic Pteropodidae species are currently listed as Vulnerable on the IUCN Red List and populations are in decline due to anthropogenic threats (Golden et al. 2014; Brook et al. 2019), and they therefore require urgent research and conservation attention (Racey 2016; Andrianaivoarivelo et al. 2019; Andriafidison et al. 2020). Pteropodidae distribution is strongly influenced by both climate and the availability of suitable habitat (Arumogum et al. 2019; Vogeler and Tschapka 2021; Diengdoh et al. 2022; Ahmed et al. 2023; Kingston et al. 2023), and the loss of natural habitats, such as forests, can severely limit Pteropodidae geographic distribution, resulting in population decline (Daniel et al. 2017; Kingston et al. 2023). Using climatic and eco-geographical variables, we constructed ENMs to investigate the distribution of three endemic Pteropodidae throughout the whole of Madagascar. Furthermore, we analysed the forest cover within their suitable land area, as fruit bats require forests for roosting and feeding. The specific research questions and objectives are therefore:

1. To determine the environmental variables that drive the geographic distribution of each Pteropodidae species. We hypothesized that different variables would limit the suitable habitat area of each species (as in Raxworthy et al. 2007; Hending 2021) and we predicted that the area identified as suitable for Pteropodidae in our models would be much larger than the actual available forest area, which they require for roosting and foraging.
2. To determine the area of forest, and area within protected areas, within the overall fundamental niche area. Taking into account the large-scale deforestation, habitat fragmentation, and climate change threats impacting Madagascar's forests (Harper et al. 2007; Vieilledent et al. 2018; Hending et al. 2022a), we hypothesized that the forest area currently available to each species would be reduced compared to the protected area and the total area of their respective ENMs. Deforestation could be the cause of their declining populations, beside the already known impact of the fruit bat bushmeat trade (Racey et al. 2009).

Methods

Study area

Madagascar is located in the Indian Ocean off the coast of southern Africa and is the second largest island state in the world. The tropical climate of the island consists of a dry season from May to October and a rainy season from November to April (Jury et al. 2022). The west coast is characterised by large dry sedimentary basins including karst plateaux, various limestone and sandstone formations, caverns and caves (Wilmé et al. 2006). The forests are sub-humid and mainly dry, while the eastern slope of Madagascar harbors humid evergreen forests. The high level of endemism is mostly represented in the forest species, including 90% of Malagasy land mammals, and almost 78% of bird species (Wilmé et al. 2006).

Pteropodidae occurrence data

Pteropodidae geographic occurrence points were collated from both published and unpublished sources. First the complete catalog of published articles in the bat-specific journals *Acta Chiropterologica* and *Journal of Bat Research & Conservation* were checked, as well as the journals with a Madagascar-focus: *Malagasy Nature* and *Madagascar Conservation and Development* (following Hending 2021). This way ensured not to miss any Pteropodidae occurrence points from the journals which might not appear in literature databases (e.g., *Malagasy Nature*). Further occurrence data was searched in non-Chiroptera-specific journals and dissertations in the online databases of Google Scholar, Web of Science and ResearchGate and in edited book volumes, particularly Goodman et al. (2018). Used keywords in online searches were “distribution”, “presence”, “population”, “occurrence”, “fruit bat” and “Pteropodidae”, in addition to the scientific and common names of the Pteropodidae species. The sampling was completed by obtained unpublished occurrence records, which are included in the most recent IUCN Red List of the three species (Racey 2016; Andrianaivoarivelo et al. 2019; Andriafidison et al. 2020). Sample sizes of 92 (*P. rufus*), 36 (*E. dupreanum*) and 68 (*R. madagascariensis*) occurrence points resulted (Fig. 1), which were all recorded in a database.

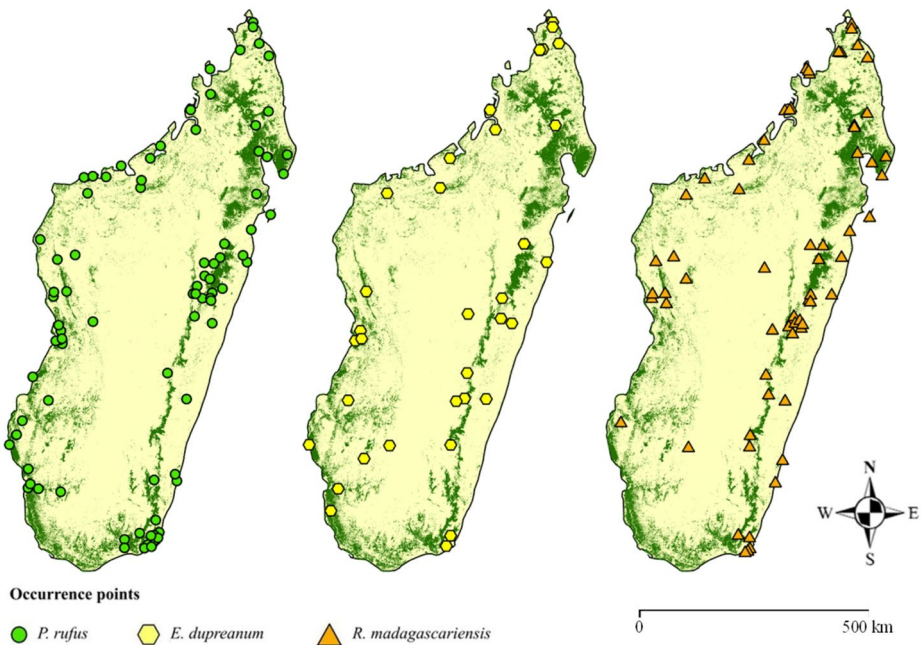


Fig. 1 Sampled occurrence points of endemic Pteropodidae in Madagascar (*Pteropus rufus* (green dots, $N=92$), *Eidolon dupreanum* (yellow hexagons, $N=36$) and *Rousettus madagascariensis* (orange triangles, $N=68$) in relation to Madagascar’s remaining forest cover (dark green: Vieilledent et al. 2018). Figure created in ArcMap, with a scale of 1: 7,000,000 for Madagascar

Environmental raster layers

Pteropodidae ENMs were constructed based on a consideration of 22 different environmental variables (Table 1). 19 of them are bioclimatic measures of climatic seasonality, temperature and precipitation (Hijmans et al. 2005), while three variables represent vegetation-cover and forest quality. These are Primary Productivity (NPP), the Normalized Difference Vegetation Index (NDVI), which is another proxy of plant productivity (Rouse et al. 1974) and the Leaf Area Index (LAI) which is a proxy of tree cover density (Asner et al. 2003). As the resolution of the data was variable (0.50–1.00 km²), resampling to the least-fine raster of 1 km² was executed in R Studio using the packages ‘raster’ (Hijmans 2023) and ‘magrittr’ (Bache and Wickham 2022). They were then projected to the WGS84 geographic coordinate system, and the raster layers were cropped to the extent of Madagascar (latitude: 11.5°–26.0°, longitude extent: 43.0–51.0°) and resampled to action script communication (ASC) format. The NDVI, LAI and NPP rasters were means of monthly layers from 2019. In ENMs, multicollinearity often exists among independent variables included as environmental layers (O’Brien 2007) and highly correlated variables should not be used together (Merow et al. 2013). We extracted the raster value of all layers from 2,000 randomly generated geographic points from Madagascar’s terrestrial land surface and checked the correlation of the variables. If the correlation coefficient was high (≥ 0.70), only one variable was chosen to use in the model, but both included, if they were particularly relevant to the ecology of Pteropodidae (Andrianaivoarivelo et al. 2022). Following these steps, the number of

Table 1 Environmental variables considered as raster layers for the construction of the Pteropodidae ecological niche models. Selected variables for modelling in maxent are marked with an asterisk (*)

Variable	Definition	Source
Bio1	Annual mean temperature (°C)	worldclim.org
Bio2	Mean diurnal range (mean (period max - min)) (°C)	worldclim.org
Bio3*	Isothermality (Bio2/Bio7) (°C)	worldclim.org
Bio4*	Temperature seasonality (SD × 100)	worldclim.org
Bio5*	Max temperature of warmest month (°C)	worldclim.org
Bio6*	Min temperature of coldest month (°C)	worldclim.org
Bio7*	Temperature annual range (Bio5 - Bio6)	worldclim.org
Bio8	Mean temperature of wettest quarter (°C)	worldclim.org
Bio9	Mean temperature of driest quarter (°C)	worldclim.org
Bio10	Mean temperature of warmest quarter (°C)	worldclim.org
Bio11	Mean temperature of coldest quarter (°C)	worldclim.org
Bio12*	Annual precipitation (mm)	worldclim.org
Bio13	Precipitation of wettest period (mm)	worldclim.org
Bio14*	Precipitation of driest period (mm)	worldclim.org
Bio15*	Precipitation seasonality (coefficient of variation)	worldclim.org
Bio16	Precipitation of wettest quarter (mm)	worldclim.org
Bio17	Precipitation of driest quarter (mm)	worldclim.org
Bio18	Precipitation of warmest quarter (mm)	worldclim.org
Bio19	Precipitation of coldest quarter (mm)	worldclim.org
LAI*	Leaf area index	neo.sci.gsfc.nasa.gov
NDVI	Normalized difference vegetation index	neo.sci.gsfc.nasa.gov
NPP	Net Primary Productivity	neo.sci.gsfc.nasa.gov

environmental variables for inclusion in the ENMs was reduced from 22 to nine (Table 1) and multicollinearity was avoided.

The selected variables represent climatic seasonal differences between geographic regions (Bio3: as in Arumoogum et al. 2019; Bio4, Bio7, Bio12 and Bio15: Dewar and Richard 2007), water availability (Bio12) and include factors which limit the distribution of Pteropodidae (Kingston et al. 2023). We chose to keep the values of maximum temperature of the warmest month (Bio5) as a population determining factor, because fruit bats cannot tolerate extreme heat and die in high temperatures (Welbergen et al. 2008; Bishop et al., 2018). Pteropodidae also do not tolerate very cold temperatures (Kingston et al. 2023), which led us to include Bio6, which can be considered a proxy of frost (Blair et al. 2013). *P. rufus* does not roost in caves (Wilson and Mittermeier 2019), and therefore does not occur in very cold areas, but has been found in temperatures ranging between 12 and 33 °C (Bollen and Van Elsacker 2002). Distribution shifts into regions with less frosty nights due to changes in mean temperature induced by climate change have already been observed in *P. alecto* in Australia (Welbergen et al. 2008). Also, we selected the variables representing potential instances of drought (Bio14) (Blair et al. 2013), which influences the availability of fruit and nectar (Aziz et al. 2021). Further, the selection should enable MaxEnt to distinguish between the different forest types that each Pteropodidae species has preference for. *P. rufus* roosts only in trees and therefore needs a high vegetation cover to escape strong heat (Welbergen et al. 2008; Wilson and Mittermeier 2019). Consequently, the Leaf Area Index (LAI) was chosen, a ratio of the total leaf area to the ground surface, as it is a good proxy for Madagascar's different ecosystems and forest habitat types (Kamilar and Muldoon 2010).

MaxEnt ecological niche model construction

We used the maximum entropy model (MaxEnt version 3.4.4; Phillips et al. 2006) to construct ENMs for the three species. The first step was to identify the individual optimal MaxEnt model features, settings and regularisation parameters (Muscarella et al. 2014) (Table 2), based on the Akaike Information Criteria (AIC). We used the R package 'ENMeval' (Kass 2023) to create bias-files, to control for spatial sampling bias and autocorrelation within the geographic range of each species, (Dudík et al. 2005). Sampling bias can have various causes, including site access difficulties, which can result in clusters of occurrence points (Hijmans et al. 2000; Reddy and Dávalos 2003; Kadmon et al. 2004). Also, surveys conducted over a long period by various researchers with different techniques and intensity can result in sampling bias (Soberón and Peterson 2004). Many species like *E. dupreanum* are known from a limited number of localities, which limits the modelling of their full niche (Wisz et al. 2008; Anderson and Gonzales, 2011). Although, as Pteropodidae are threatened by many factors (Andrianiaina et al. 2022), some occurrence points may represent a suitable area where they can survive in comparison to their preferred habitat (Egert-Berg et al. 2021).

For the MaxEnt models, a four-fold sampling method, proven successful for low numbers of occurrence points ($N < 50$: Pearson et al. 2007; Peterson et al. 2011) was used via a cross-validation technique (as in de Almeida et al. 2019). The maximum number of iterations was set to 500 on 10,000 randomly generated background points and a convergence threshold of 0.001 (as in Tran et al. 2018). Sufficient occurrence points (*P. rufus*: $N = 92$, *E.*

Table 2 Construction of four-fold ENMs of the three Pteropodidae species endemic to Madagascar in maxent: total number of occurrence points (N), feature parameters (L=Linear, Q=Quadratic, P=Product, T=Threshold, H=Hinge) and regularization multipliers used. AUC values and binomial tests of omission for *Eidolon Dupreanum* aren't convincing features for the accuracy and validity of the maxent ENMs

Pteropodidae Species	Total OccurrencePoints (N)	Features Included	Regularization Multiplier	Mean Test AUC (Rrange)	Test AUC SD (Range)	Omission Error MTP			
						Fold 1	Fold 2	Fold 3	Fold 4
<i>P. nifus</i>	92	LQHPT	2	0.731 (0.700–0.773, 700.773)	0.044 (0.038–0.051)	0.261 P=0.012	0.227 P=0.003	0.046 P<0.001	0.227 P<0.001
<i>E. dupreanum</i>	36	L	0.5	0.669 (0.589–0.790)	0.104 (0.084–0.129)	0.111 P=0.084	0.444 P=0.550	0.250 P=0.363	0.125 P=0.440
<i>R. madagascariensis</i>	68	LQ	1.5	0.794 (0.714–0.848)	0.040 (0.030–0.058)	0.118 P<0.001	0.294 P=0.007	0.063 P<0.001	0.063 P<0.001

dupreanum: $N=36$, *R. madagascariensis*: $N=68$) were sampled of all Pteropodidae to construct ENMs (Hernandez et al. 2006), and we used 80% of the points as training data and 20% as test data. The significance of each model-fold's prediction was calculated by using binomial tests of omission to further validate the models (as in Blair et al. 2013; Bellamy and Altringham 2015; Grimshaw et al. 2021).

MaxEnt ENM evaluation and validation

The area under the response curve (AUC) was used to evaluate each individual ENM's performance. The AUC method penalizes prediction beyond known occurrence locations, thus minimizing overfitting of a model (Merow et al. 2013). In review of other studies, we determined that models with an AUC score >0.7 were considered reliable (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011; Blair et al. 2013; Fuchs et al. 2018). Models are always influenced by non-independent factors and approximations (Lobo et al. 2008). The AUC method ignores the predicted probability values and the models' goodness-of-fit, and so it should be used in combination with other validation methods. We therefore also conducted binomial omission tests. These tests are sensitive to proportional predicted area (Anderson et al. 2003), and we considered them statistically significant if the P -value was 0.05 or lower (as in Bellamy and Altringham 2015).

Spatial and statistical analysis

The ENMs were loaded into ArcGIS Pro (version 3.0, Esri, Redlands CA, USA) and we applied a binary threshold based on the MaxEnt output to distinguish between suitable vs. unsuitable habitat (as in Blair et al. 2013; McDonald et al. 2019; Scherrer et al. 2019). We assumed that occurrence records in the least suitable habitat are not representative of the species overall habitat. Due to hunting pressure, the loss of habitat and available food as a result of the high rate of deforestation (Andrianiaina et al. 2022; Suzzi-Simmons 2023), the animals could move to less suitable areas. To omit these areas, a 10th percentile training presence (P10) threshold was applied, which excludes the lowest 10% of occurrence points and thus all regions with lower habitat suitability scores. Compared to the P10 threshold, the minimum training presence (MTP) threshold assumes that the lowest predicted suitability value for an occurrence point is the minimum suitability value for the species. As the P10 threshold omits a greater region (Morrow, 2019), it is therefore a more conservative metric of suitable habitat, and minimises the risk of over-prediction. Afterwards the suitable area for each Pteropodidae was calculated. We further clipped the P10 threshold area of the ENMs with a layer of Madagascar's forest (Vieilledent et al. 2018), and we calculated how much forest area is available within the suitable habitat area of each species; Pteropodids feed on fruits and roost in trees, and they therefore depend on this forest habitat for survival (Aziz et al. 2021). This way, areas outside of forest cover could be excluded, with the remaining area representative of available roosting area. We then calculated how much of this suitable forest area was within Madagascar's protected area network, to gauge how well protected each species is within its range. To determine the potential effect of roost availability on the three species, we downloaded mean canopy height data (Lang et al. 2023), and we created a terrain ruggedness index (TRI) layer using a digital elevation model for Mada-

gascar. Canopy height is a suitable proxy of tall trees, and therefore roost availability for *P. rufus*, while TRI is a suitable proxy of cave occurrence for the cave roosting *E. dupreanum* and *R. madagascariensis* (Wilson and Mittermeier 2019). For each species, we generated 1000 random geographic points within both its suitable and unsuitable habitat area using the threshold ENMs. For each point, we extracted canopy height (*P. rufus*) and TRI data (*E. dupreanum* and *R. madagascariensis*), which we then checked for normality using Shapiro-Wilks tests. All three species roost proxy datasets were of non-normal distribution (*P. rufus*: $W=0.968$, $P<0.001$; *E. dupreanum*: $W=0.999$, $P=0.026$; *R. madagascariensis*: $W=0.998$, $P=0.025$), so we compared the roost availability proxies between each species' suitable and unsuitable habitat areas using Mann-Whitney U tests.

Results

ENM performance

The ENM AUC values of 0.669–0.794 suggest that model performance was fair to good: *P. rufus* AUC=0.731, *E. dupreanum* AUC=0.669 and *R. madagascariensis* AUC=0.794 (Table 2). However, the MaxEnt ENMs of all three species produced maps representative of the known geographic ranges of each species (Fig. 2). To further validate the performance of the individual ENMs, the statistical significance of the binomial tests of omission of the models four-fold predictions were checked. They highlight the validity and high performance of the models for *P. rufus* and *R. madagascariensis* (Table 2). None of the tests were significant for *E. dupreanum*, so this ENM cannot be considered reliable enough to draw any robust conclusion for the species habitat requirements. However, the model is useful for highlighting as-yet unsurveyed areas where this species may occur, and therefore studied in

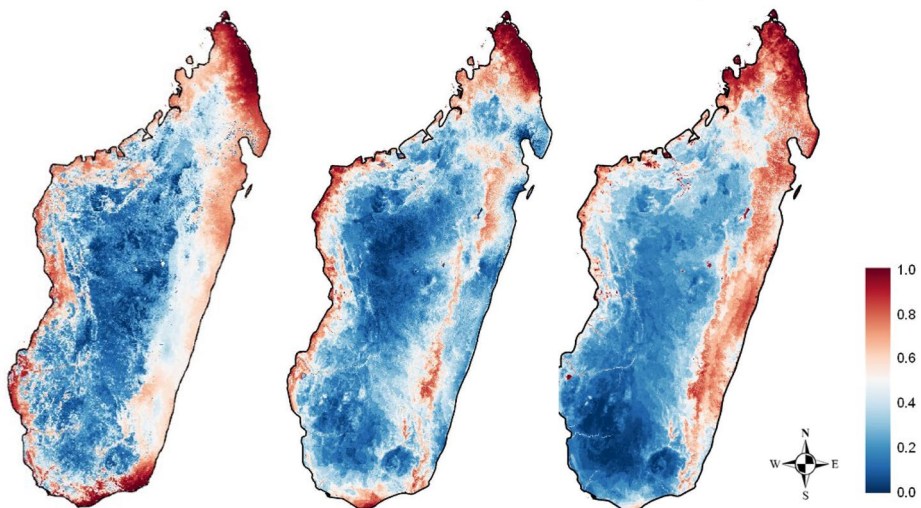


Fig. 2 The ENMs showing suitable (red) and unsuitable areas (blue) of *P. rufus* (left), *E. dupreanum* (middle), *R. madagascariensis* (right). The color scheme ranges from unsuitable (0) to very suitable (1). Figure created in ArcMap, with a scale of 1: 7,000,000 for Madagascar

Table 3 Percentage contributions of each environmental layer to maxent ENMs of the three fruit Bat species. Bio3: isothermality (°C), Bio4: temperature seasonality, Bio5: maximum temperature of warmest month (°C), Bio6: minimum temperature of coldest month (°C), Bio7: temperature annual range, Bio12: annual precipitation (mm), Bio14: precipitation of driest period (mm), Bio15: precipitation seasonality, LAI: leaf area index

Variable	Percent contribution (%)		
	<i>P. rufus</i>	<i>E. dupreanum</i>	<i>R. madagascariensis</i>
Bio3	2.4	4	1.2
Bio4	2	0.7	0.6
Bio5	0	3.7	0
Bio6	8.1	16.1	3.9
Bio7	4	40.5	62.5
Bio12	12.3	22.9	2.3
Bio14	4.4	4	3.7
Bio15	19.6	0.2	0.4
LAI	47.2	7.7	25.3

Table 4 The 10th percentile training presence (P10) threshold of each Pteropodidae maxent ENM, the suitable area (km²) of occupancy of the three Pteropodidae species, the area and percentage of forest habitat and the area and percentage of forest habitat that is protected

Pteropodidae Species	P10 Threshold	Threshold area (km ²)	Forest area (km ²)	Protected forest area (km ²)
<i>P. rufus</i>	0.4508	228,429	52,170 (22.8%)	40,313 (17.7%)
<i>E. dupreanum</i>	0.3857	280,989	54,636 (19.4%)	40,996 (14.6%)
<i>R. madagascariensis</i>	0.4473	197,171	40,647 (20.6%)	33,505 (20.6%)

the future, and from where additional occurrence points may be obtained for future modeling work. Among the three species the percentage contribution of the nine environmental variables varied and the most influential were LAI for *P. rufus*, and Bio 7 for both *E. dupreanum* and *R. madagascariensis* (Table 3).

Spatial analysis

Spatial analysis of the ENMs in ArcGIS resulted in a range from 197,171 to 280,989 km² (mean=239,080 km²) of suitable area available for each Pteropodidae species (Table 4). Only 40,647 to 54,636 km² (mean=47,642 km²) of this territory is forest covered (Table 4), and from that 33,505 to 40,996 km² (mean=37,251 km²) is within Madagascar's protected area network (Table 4). As Pteropodidae roost in trees and in caves surrounded by forest (Wilson and Mittermeier 2019), the niche used is limited to the suitable forested habitat with a mean of 21.1% (range=19.4–22.8%, Table 4) of their projected P10 threshold area. The available suitable area for *P. rufus* was 228,429 km² and the area of forest 52,170 km², which means 22.8% of the total P10 threshold area is forested (Fig. 3; Table 4). From the forested area suitable for *P. rufus*, 40,313 km² (17.7%) is within Madagascar's protected area network (Fig. 3; Table 4). For *E. dupreanum* it was 280,989 km² suitable area and 54,636 km² (19.4%) of that is forested, while 40 996 km² (14.6%) is within Madagascar's protected area network. The ENM for *R. madagascariensis* projected 197,171 km² suitable P10 area, a forest cover of 40,647 km² (20.6%) and protected is 33 505 km² (20.6%) (Figs. 3 and 4; Table 4).

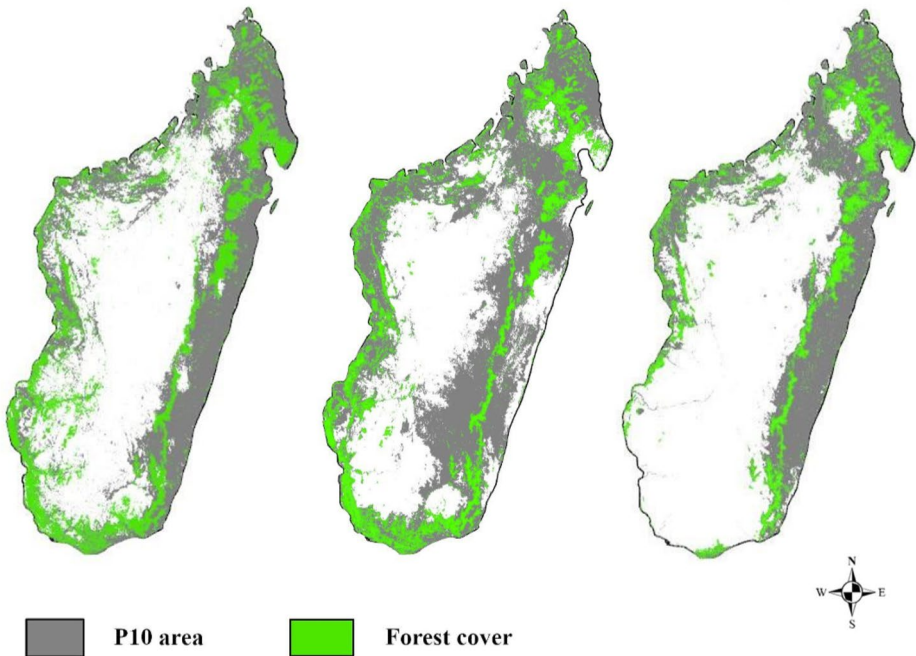


Fig. 3 Forest cover (green) within the P10 threshold area (dark grey) of the ENMs: *P. rufus* (left), *E. dupreanum* (middle), *R. madagascariensis* (right). Figure created in ArcMap, with a scale of 1: 7,000,000 for Madagascar

Mean canopy height, a proxy of tree roost availability for *P. rufus*, was significantly higher ($W=363868$, $P<0.001$) in suitable habitat areas for this species (mean=15.06 m) in comparison to unsuitable habitat areas (mean=10.00 m). Terrain ruggedness index (TRI), a proxy of cave roost availability for *E. dupreanum* and *R. madagascariensis*, was significantly higher for both species (*E. dupreanum*: $W=466632$, $P=0.009$; *R. madagascariensis*: $W=457704$, $P=0.001$) in suitable habitat areas (*E. dupreanum* mean TRI=0.478, *R. madagascariensis* mean TRI=0.482) in comparison to unsuitable habitat areas (*E. dupreanum* mean TRI=0.467, *R. madagascariensis* mean TRI=0.466).

Discussion

ENM performance

The ENMs for all three Pteropodidae species represented their known geographic distribution (Fig. 5). The validity of the models can be confirmed by the binomial omission test results and the AUC values of >0.700 for *P. rufus* and *R. madagascariensis*. We expected the AUC value for *E. dupreanum* to be the lowest between the three species, because of its lowest number of occurrence points and its broad distribution throughout the island (Table 2). As *E. dupreanum* also has non-significant binomial tests (Table 2), the ENM for this species cannot be considered reliable enough to draw robust conclusions about its habitat prefer-

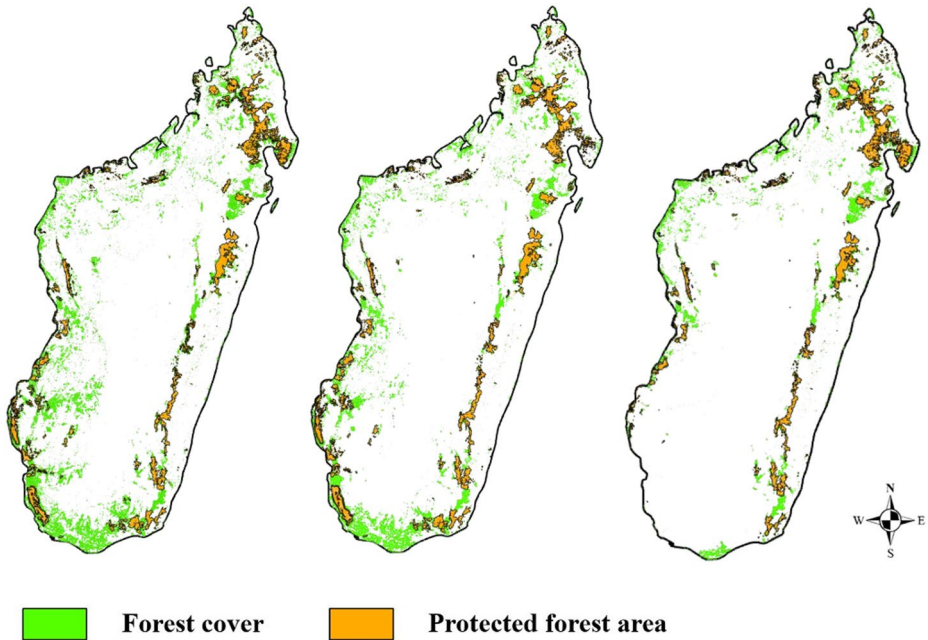


Fig. 4 Protected forest cover (orange), of total forest cover (green) within the P10 threshold area of the ENMs: *P. rufus* (left), *E. dupreanum* (middle), *R. madagascariensis* (right). Figure created in ArcMap, with a scale of 1: 7,000,000 for Madagascar

ences and conservation assessment. However, the ENM of *E. dupreanum* highlights the areas which are suitable for the species and could serve to facilitate further fieldwork, so it is included for completeness. Sampling bias may have had an influence on the ENMs, as the known occurrence points may not include roost sites difficult to reach by researchers.

Pteropodidae use a large area for foraging around their resting places and utilise different habitats depending on the season (Wilson and Mittermeier 2019; Aziz et al. 2021). As the three species cover many forest habitat types (i.e., dry forest, humid forest, transitional forest, spiny forest) over a large climatic range, MaxEnt may differentiate less effectively between suitable vs. unsuitable areas than in comparison for species with more specialized and narrower niches and habitat preferences (Zhao et al. 2011). Consequently, model evaluation metrics are less suitable to assess ENMs of wide-ranged species, including generalists like Pteropodidae (Kingston et al. 2021; Zhao et al. 2011). Applying a threshold might minimize false negatives results in a significant increase of false positives for presence and absence classification. However, the model for *E. dupreanum* was the one with the highest suitable land area (Table 4). This could result from extreme hunting pressure which promotes migration and dispersal (Hayman and Peel 2016) in potentially less preferred habitats (Wilson and Mittermeier 2019). All ENMs include some areas outside of the currently known geographic ranges (Fig. 5), but still reliably depict the area that each Pteropodidae species can theoretically occupy.

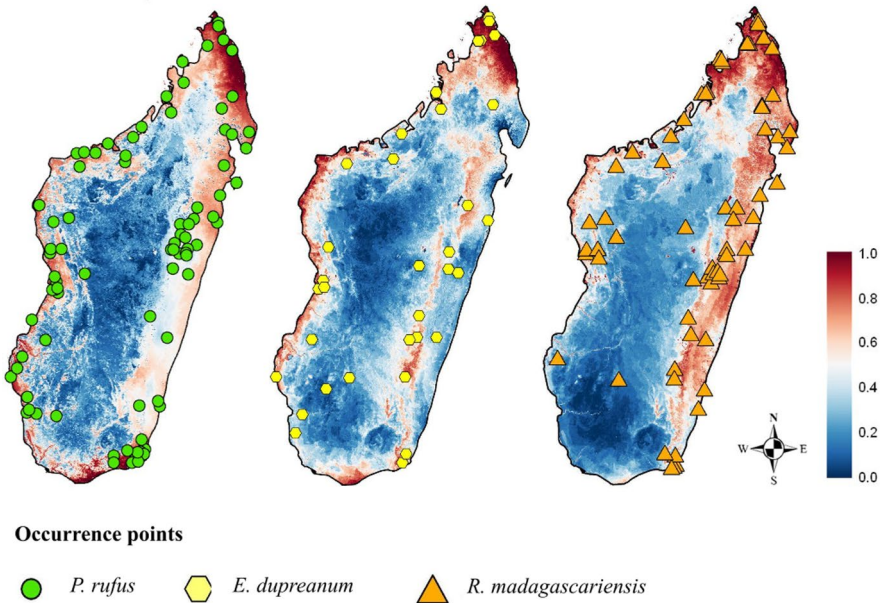


Fig. 5 Sampled occurrence points of endemic Malagasy Pteropodidae clipped to the ENM's (*Pteropus rufus* (left, green dots, $N=92$), *Eidolon dupreanum* (middle, yellow hexagons, $N=36$) and *Rousettus madagascariensis* (right, orange triangles, $N=68$). The ENM's color scheme ranges from unsuitable (0) to very suitable (1) area. Figure created in ArcMap, with a scale of 1: 7,000,000 for Madagascar

Environmental determinants

The ENM variable percentage contribution shows some similarities in the different species habitat and environmental characteristics (Table 3). A climatic variable (Bio7: temperature annual range) was the principal determinant of the distribution of *E. dupreanum* and *R. madagascariensis* (Table 3). Pteropodidae cannot tolerate either extreme cold or hot temperatures (Kingston et al. 2023) and they depend on fruits and nectar for food across the whole year (Bollen and Van Elsacker 2002; Bollen et al. 2004; Aziz et al. 2021). The species are threatened by habitat loss due to fire, logging and clearing for agriculture, and hunting for bushmeat (MacKinnon et al. 2003). This makes the mean temperature an important environmental factor. They may switch to nightly foraging on very hot days, but on hot nights their metabolic rates can be 2–3 times higher during flight as similar-sized mammals (Thomas 1975). Hyperthermia during flight has been recorded in *P. poliocephalus* at temperatures around 25 °C (Carpenter 1986). This means that they cannot compensate for the loss of water and nutrients on hot days by foraging at night (Kingston et al. 2023). As they rely on fruits for their water supply, quick dehydration and energy depletion are risks for Pteropodidae (Kingston et al. 2023). Heat is therefore a distribution influencing factor, which shifts populations into regions with less cold nights, but also a higher risk of heat. (Welbergen et al. 2008). Pteropodids do not sweat and can only cool themselves to a limited extent by flapping their wings (Welbergen et al. 2008). They are homoiothermic, and migrate to warmer areas in winter or cluster as a thermoregulatory mechanism against cold (Lučan et al. 2016; Kingston et al. 2023). As *P. rufus* is absent from highlands (Fig. 1) where it is colder than

on the coasts (Jury et al. 2022), low temperatures may have a higher impact on this strictly tree-roosting species, in comparison to *E. dupreanum* and *R. madagascariensis* which may escape the cold by also roosting in forest caves and caverns (Wilson and Mittermeier 2019). We found that terrain ruggedness, a proxy of cave presence, was higher in suitable habitat areas of *E. dupreanum* and *R. madagascariensis* in comparison to unsuitable area. This suggests that the availability of suitable cave roosts may be a limiting factor in the distribution of these two species. Dense tree crowns protect *P. rufus* from environmental influences and threats (Oleksy et al. 2015), mostly outside protected areas but also in relatively intact, but fragmented forests (Jenkins et al. 2007), and this consequently may have resulted in the high contribution of the leaf area index variable (a proxy of tree cover density) to the model of this species. The results of our mean canopy height analysis support this, with mean canopy height (a proxy of tall tree presence) being greater in suitable habitat areas for *P. rufus* in comparison to unsuitable areas. Further, ongoing deforestation will decrease the availability of suitable roost trees (trees with large crowns) for *P. rufus*; as this species depends on such trees for roosts, their distribution will likely be restricted to areas with no deforestation and minimal habitat degradation (Rahaingodrahety et al. 2008; Meyer et al. 2016). Neither very high nor cold temperatures are suitable for Pteropodids (Kingston et al. 2023). Presumably due to the ability of Pteropodidae to fly to new regions and habitats, maximum temperature contributed a very low percentage to the models. Forest cover is an important factor especially for *P. rufus*, which does not seek shelter in caves. However, Pteropodidae behaviour can differ significantly depending on environmental factors, and further research on the species behaviour that considers the importance of background conditions and contexts must be carried out (Egert-Berg et al. 2021).

Spatial analysis

The clipped forest raster layers underpin the importance of differentiating the fundamental niche from the realised niche and therefore produce a more-accurate projection of suitable areas for Pteropodids. ENMs often include habitat types where the species will not occur (Peterson et al. 2007; Mendes et al. 2020). As Pteropodids roost in trees and caves surrounded by forest (Wilson and Mittermeier 2019), such as in the Ankarana National Park cave system (Cardiff et al. 2009, 2012), their suitable habitat area (i.e., their realised niche) is reduced to the forest area within the threshold-clipped ENMs, which is only around 21.1% of the fundamental niche area (mean=47,642 km², Table 4). This available forest habitat is a conservative estimate of available habitat. More conservative models are always preferable to underpredicted models when looking at conservation statuses, as they lean towards a worst-case scenario instead of glossing over a potential problem (Peterson et al. 2007; Mendes et al. 2020). In addition, only a mean of 17.6% (range=14.6–20.6%, Table 4) of the suitable forest area is under protection.

Areas where Pteropodids could theoretically occur are larger than the known geographical distribution. Concluding that, the area of forest habitat available to each species is lower, which therefore warrants these species' current IUCN Red List statuses of Vulnerable (Racey 2016; Andrianaivoarivelo et al. 2019; Andriafidison et al. 2020), particularly considering that deforestation is still occurring throughout Madagascar (Suzzi-Simmons 2023). Although *E. dupreanum* persists in modified landscapes with little forest cover and large human populations, faecal analysis of populations close to humid forests show a more

diverse diet and therefore a higher influence on seed dispersal of forest plants (Picot et al. 2007). In comparison, *P. rufus* has a strong forest-roost-site selection and is more sensitive to anthropogenic disturbance (Racey et al. 2009). An extension of the protected forest area to the suitable forest area would be beneficial for Pteropodids conservation, and ensure the future of Madagascar's threatened animals (Goodman et al. 2018). We suggest preventing deforestation and also undertaking reforestation efforts are both suitable conservation strategies. As Pteropodids pollinate plants and disperse seeds (Aziz et al. 2021), these strategies could contribute to ensure the future of their ecosystem services.

Study limitations

Although the ENMs performed reliably, the AUC score was lower than 0.7 for *E. dupreanum*, likely due to its wide distribution and low number of occurrence points. For generalist species, increasing the number of occurrence points may allow MaxEnt to distinguish more easily among presence and absence points, thus increasing AUC values (Lobo et al. 2008). Also, a higher performance can result by adjusting model parameters to include features which we were not able to (e.g. hinge features) due to the small number of occurrence points of *E. dupreanum* (Anderson and Gonzalez 2011; Radosavljevic and Anderson 2014). For some environmental variables, the smallest resolution available was 1 km². A finer resolution may improve the accuracy of the MaxEnt models (Ross et al. 2015) and identify additional environmental variables that influence the distributions. Despite these limitations, the models are highly useful for understanding each species distribution and habitat areas, for conservation assessments, planning future studies and fieldwork (Ramoni-Perazzi et al. 2012; Arumoogum et al. 2019; Bandara et al. 2022).

Implications and conclusions

Pteropodidae provide important ecosystem services within the biodiversity hotspot of Madagascar (Wunderle 1997; Andriafidison et al. 2006; Aziz et al. 2021), but have a very limited available habitat for their distribution. This study identified suitable forest tracts for the three endemic Pteropodids and its proportion within Madagascar's protected area network. The annual temperature range (*E. dupreanum*, *R. madagascariensis*) and tree cover density (LAI) (*P. rufus*) were the most important variables that determine the Pteropodids distribution. These results can be useful to determine places for further ecological studies and estimating the population sizes, as well as for assessing species conservation status. Furthermore, they can serve to investigate potential niches under future climate scenarios. Despite their presence in a range of different habitat types, knowledge on the distribution of Madagascar's bats remains limited (Goodman et al. 2005; Kofoky et al. 2007; Kemp et al. 2019; Hending et al. 2021b, 2022b). Whilst this study begins to address this issue for the Pteropodidae, similar efforts are needed for insectivorous bats, many of which are also highly dependent on forest habitat for foraging and roosting (Randrianandrianina et al. 2006; Rakotoarivelo et al. 2007; Kofoky et al. 2009; Goodman et al. 2014). As Madagascar's forests remain threatened by deforestation, degradation, and edge-effects (Harper et al. 2007; Vieilledent et al. 2018; Hending et al. 2023c), such data is urgently required. It will be not only vital for the conservation of Madagascar's bat populations, but also to other threatened species due to their ecosystem services Seed dispersal and pollination by

Pteropodids can support reforestation (Wunderle 1997; Bello et al. 2021) and thus may counteract drought and the effects of climate change.

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Declarations

Competing interests The authors declare no competing interests.

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References

- Abrol DP (2012) Pollination biology: biodiversity conservation and agricultural production, vol 792. Springer, New York
- Aguiar LMS, Pereira MJR, Zortéa M, Machado RB (2020) Where are the bats? An environmental complementarity analysis in a megadiverse country. *Divers Distrib* 26:1510–1522. <https://doi.org/10.1111/ddi.13108>
- Ahmed AS, Bekele A, Kasso M, Atickem A (2023) Impact of climate change on the distribution and predicted habitat suitability of two fruit bats (*Rousettus aegyptiacus* and *Epomophorus labiatus*) in Ethiopia: implications for conservation. *Ecol Evol* 13(9):e10481
- Allnutt TF, Ferrier S, Manion G, Powell GV, Ricketts TH, Fisher BL et al (2008) A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. *Conserv Lett* 1(4):173–181. <https://doi.org/10.1111/j.1755-263X.2008.00019.x>
- Anderson RP, Gonzalez I (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with maxent. *Ecol Model* 222(15):2796–2811. <https://doi.org/10.1016/j.ecolmodel.2011.07.019>
- Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecol Model* 162(3):211–232. [https://doi.org/10.1016/S0304-3800\(02\)0349-6](https://doi.org/10.1016/S0304-3800(02)0349-6)
- Andriafidison D, Andrianaivoarivelo RA, Ramilijaona OR, Razanahoera MR, MacKinnon J, Jenkins RKB et al (2006) Nectarivory by endemic Malagasy fruit bats during the dry season. *Biotropica* 38:85–90. <http://doi.org/10.1111/j.1744-7429.2006.00102.x>
- Andriafidison D, Andrianaivoarivelo R, Cardiff SG, Goodman SM, Hutson AM, Jenkins RKB et al (2020) Eidolon dupreanum. The IUCN red list of threatened species 2020. <https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T7083A22027891.en>. e.T7083A22027891

- Andrianaivoarivelo R, Andriafidison D, Razafimanahaka J (2019) *Rousettus madagascariensis*. The IUCN red list of threatened species 2019. [https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T19750A22002909](https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T19750A22002909.en)
- Andrianaivoarivelo R, Andriafidison D, Razafimanahaka JH, Razafindrakoto N, Oleksy RZ, Racey PA et al (2022) Pteropodidae, fruit Bats, Fanihy, Angavo. In: Goodman SM (ed) The new natural history of Madagascar. Princeton University Press, Oxford, pp 1911–1917
- Andrianaina A, Andry S, Gentles A, Guth S, Héraud JM, Ranaivoson HC et al (2022) Reproduction, seasonal morphology, and juvenile growth in three Malagasy fruit bats. *J Mammal* 103(6):1397–1408. <https://doi.org/10.1093/jmammal/gyac092>
- Antonelli A, Smith RJ, Perrigo AL, Crottini A, Hackel J, Testo W et al (2022) Madagascar's extraordinary biodiversity: evolution, distribution, and use. *Science* 378(6623):eabf0869. <https://doi.org/10.1126/science.abf0869>
- Arumoozum N, Schoeman MC, Ramdhani S (2019) The relative influence of abiotic and biotic factors on suitable habitat of old world fruit bats under current and future climate scenarios. *Mamm Biol* 98:188–200. <https://doi.org/10.1016/j.mambio.2019.03.002>
- Asner GP, Scurlock JM, Hicke J (2003) Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Glob Ecol Biogeogr* 12(3):191–205. <https://doi.org/10.1046/j.1466-822X.2003.00026.x>
- Aziz SA, McConkey KR, Tanalgo K, Sritongchuay T, Low M-R, Yong JY et al (2021) The critical importance of Old World fruit bats for healthy ecosystems and economies. *Front Ecol Evol* 9:641411. <https://doi.org/10.3389/fevo.2021.641411>
- Bache S, Wickham H (2022) magrittr: A forward-pipe operator for R. R package version 2.0.3.
- Bandara APMJ, Madurapperuma BD, Edirisinghe G, Gabadage D, Botejue M, Surasinghe TD (2022) Bioclimatic envelopes for two Bat species from a tropical island: insights on current and future distribution from ecological niche modeling. *Diversity* 14:506
- Bellamy C, Altringham J (2015) Predicting species distributions using record centre data: multi-scale modeling of habitat suitability for Bat roosts. *PLoS One* 10(6):e0128440
- Bello C, Culot L, Agudelo CAR, Galetti M (2021) Valuing the economic impacts of seed dispersal loss on voluntary carbon markets. *Ecosystem Serv* 52:101362
- Bishop T, Lyons R (2018) Flying-fox heat event response guidelines SEQ. Preprints:2018090455
- Black SA (2020) Assessing presence, decline, and extinction for the conservation of difficult-to-observe species. In: Angeleici FM, Rossi L (eds) Problematic wildlife II. Springer, Cham, pp 359–392
- Blair ME, Sterling EJ, Dusch M, Raxworthy CJ, Pearson R (2013) Ecological divergence and speciation between Lemur (*Eulemur*) sister species in Madagascar. *J Evol Biol* 26(8):1790–1801
- Bollen A, Van Elsacker L (2002) Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. *Acta Chiropterol* 4(1):33–47
- Bollen A, Van Elsacker L, Ganzhorn JU (2004) Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. *J Trop Ecol* 20(6):599–612
- Boria RA, Olson LE, Goodman SM, Anderson RP (2017) A single-algorithm ensemble approach to estimating suitability and uncertainty: cross-time projections for four Malagasy Tenrecs. *Divers Distrib* 23(2):196–208
- Brook CE, Ranaivoson HC, Andriafidison D, Ralisata M, Razafimanahaka J, Héraud J-M et al (2019) Population trends for two Malagasy fruit bats. *Biol Conserv* 234:165–171
- Cabral JS, Kreft H (2012) Linking ecological niche, community ecology and biogeography: insights from a mechanistic niche model. *J Biogeogr* 39(12):2212–2224
- Cardiff SG, Ratrimomanarivo FH, Rembert G, Goodman SM (2009) Hunting, disturbance and roost persistence of bats in caves at Ankarana, Northern Madagascar. *Afr J Ecol* 47:640–649
- Cardiff SG, Ratrimomanarivo FH, Goodman SM (2012) The effect of tourist visits on the behavior of *rousettus madagascariensis* (Chiroptera: Pteropodidae) in the caves of Ankarana, Northern Madagascar. *Acta Chiropterol* 14(2):479–490
- Carpenter RE (1986) Flight physiology of intermediate-sized fruit bats (Pteropodidae). *J Exp Biol* 120(1):79–103
- Caruso N, Guerisoli M, Vidal EL, Castillo D, Casanave EB, Lucherini M (2015) Modelling the ecological niche of an endangered population of *Puma concolor*: first application of the GNESFA method to an elusive carnivore. *Ecol Model* 297:11–19
- Daniel BM, Green KE, Doulton H, Salim DM, Said I, Hudson M, Dawson JS, Young RP, Houmadi A (2017) A bat on the brink? A range-wide survey of the critically endangered livingstone's fruit bat *Pteropus Livingstonii*. *Oryx* 51(4):742–751
- de Almeida MA, Dos Santos E, Cardoso JDC, da Silva LG, Rabelo RM, Bicca-Marques JC (2019) Predicting yellow fever through species distribution modeling of virus, vector, and monkeys. *EcoHealth* 16(1):95–108

- Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. *Proc Natl Acad Sci* 104(34):13723–13727
- Diengdoh VL, Ondei S, Hunt M, Brook BW (2022) Predicted impacts of climate change and extreme temperature events on the future distribution of fruit bat species in Australia. *Glob Ecol Conserv* 37:e02181
- Dudík M, Phillips S, Schapire RE (2005) Correcting sample selection bias in maximum entropy density estimation. *Adv Neural Inf Process Syst* 18:323–330
- Egert-Berg K, Handel M, Goldshtein A, Eitan O, Borissov I, Yove Y (2021) Fruit bats adjust their foraging strategies to urban environments to diversify their diet. *BMC Biol* 19:123
- Elith JH, Graham CP, Anderson R, Dudík M, Ferrier S, Guisan AJ et al (2006) Novel methods improve prediction of species distributions from occurrence data. *Ecography* 29(2):129–151
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of maxent for ecologists. *Divers Distrib* 17(1):43–57
- Estrada-Villegas S, Stevenson PR, López O, DeWalt SJ, Comita LS, Dent DH (2023) Animal seed dispersal recovery during passive restoration in a forested landscape. *Philos Trans R Soc Lond B Biol Sci* 378(1867):20210076
- Ferrer-Sánchez Y, Rodríguez-Estrella R (2016) How rare species conservation management can be strengthened with the use of ecological niche modelling: the case for endangered endemic gundlach's Hawk and Cuban Black-Hawk. *Glob Ecol Conserv* 5:88–99
- Fialas PC, Santini L, Russo D, Amorim F, Rebelo H, Novella-Fernandez R, Marques F, Domer A, Vella A, Martinoli A, Figurek A, Tsoar A, Sandor A, Ibanez C, Korine C, Kerbirou C, Voigt C, Mifsud C, Jéré C, Ridha D, Preatoni D, Hamidović D, Tidenberg EM, Çoraman E, Mathews F, Lison F, Joanna F, Petersons G, Loumassine H, Garin I, Csósz I, Liira J, Juste J, Julien JF, van der Kooij J, Darija J, Aihartza J, Eldegar K, Phelps K, Olival KJ, Marina K, Ancillotto L, Grzegorz L, Barti L, Salazar LC, Bosso L, Rodrigues L, Hamel L, Uhrin M, Mas M, Cerekovic N, Toshkova N, Roche N, Kalda O, Aizpurua O, Georgiakakis P, Kanuch P, Presetnik P, Bilgin R, McKay RA, Dina R, Goran R, Ireneusz R, Sorås R, Robert S, Aulagnier S, Kramer-Schadt S, Gazaryan S, Bücs SL, Yorulmaz T, Stjernberg T, Liukko UM, Nistoreanu V, Vintulis V, Radchuk V, Puig-Montserrat X, Bas Y, Zagmajster M, Zegarek M, Vida Z, Razgour O (2025) Changes in community composition and functional diversity of European bats under climate change. *Conserv Biol* 39(4):e70025
- Fuchs AJ, Gilbert CC, Kamilar JM (2018) Ecological niche modeling of the genus *Papio*. *Am J Phys Anthropol* 166(4):812–823
- Ganzhorn JU, Wilmé L, Mercier JL (2014) Explaining Madagascar's biodiversity. *Conservation and Environmental Management in Madagascar*. Routledge, pp 17–43
- Garbino GST, Pessoa da Silva F, Gonçalves da Silva L (2023) Distribution, habitat suitability, and revised morphological diagnosis confirm that the fruit Bat *Platyrrhinus recifinus* is an Atlantic forest endemic. *Stud Neotrop Fauna Environ* 58(2):344–355
- Golden CD, Bonds MH, Brashares JS, Rodolph Rasolofoniaina BJ, Kremen C (2014) Economic valuation of subsistence harvest of wildlife in Madagascar. *Conserv Biol* 28:234–243
- Gonçalves F, Sales LP, Galetti M, Pires MM (2021) Combined impacts of climate and land use change and the future restructuring of Neotropical bat biodiversity. *Perspect Ecol Conserv* 19(4):454–463
- Goodman SM, Andriafidison D, Andrianaivoarivelo R, Cardiff SG, Ifticene E, Jenkins RK et al (2005) The distribution and conservation of bats in the dry regions of Madagascar. *Anim Conserv* 8(2):153–165
- Goodman SM, Rasoanoro M, Ralisata M, Ramasindrazana B (2014) The bats of the Kianjavato-Vatovavy region, lowland Eastern central Madagascar. *Malagasy Nat* 8:89–102
- Goodman SM, Raheirilalao MJ, Wohlhauser S (2018) The terrestrial protected areas of Madagascar: their history, description, and biota. University Press, Association Vahatra, Antananarivo, pp 701–715
- Grimshaw JR, Ray DA, Stevens RD (2021) Ecological niche models for Bat species of greatest conservation need in Louisiana. *Museum Texas Tech University Occasional Papers*, p 378
- Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. *Environ Conserv* 34(4):325–333
- Hayman DT, Peel AJ (2016) Can survival analyses detect hunting pressure in a highly connected species? Lessons from straw-coloured fruit bats. *Biol Conserv* 200:131–139
- Hending D (2021) Niche-separation and conservation biogeography of Madagascar's fork-marked lemurs (Cheirogaleidae: *Phaner*): evidence of a new cryptic species? *Glob Ecol Conserv* 29:e01738
- Hending D (2025) Cryptic species conservation: a review. *Biol Rev* 100(1):258–274
- Hending D, Randrianarison H, Holderied M, McCabe G, Cotton S (2021a) The kapok tree (*Ceiba pentandra* (L.) Gaertn, Malvaceae) as a food source for native vertebrate species during times of resource scarcity and its potential for reforestation in Madagascar. *Austral Ecol* 46:1440–1444
- Hending D, Drew H, Holderied MW (2021b) Habitat use of constant frequency echolocating bats in north-west Madagascar with acoustic evidence for a possible new species. *Acta Chiropterol* 23(1):153–164

- Hending D, Holderied M, McCabe G, Cotton S (2022a) Effects of future climate change on the forests of Madagascar. *Ecosphere* 13:e4017
- Hending D, Andrianiaina A, Rose M, Rowlands A, Storm S, Holderied MW, Cotton S (2022b) Vanilla bats: insectivorous bat diversity in the vanilla agroecosystems of northeastern Madagascar. *Acta Chiropterol* 24(2):363–378
- Hending D, McCabe G, Cotton S, Holderied M (2023a) Conservation biogeography of the dwarf lemurs (*Cheirogaleus*) of Madagascar, investigated via ecological niche modelling. *Int J Primatol* 44(5):960–983
- Hending D, Andrianiaina A, Rakotomalala Z, Cotton S (2023b) Conservation value of vanilla agroecosystems for vertebrate diversity in north-east Madagascar. *Oryx* 57(1):118–128
- Hending D, Randrianarison H, Andriamavosoloarisoa NNM, Ranohatra-Hending C, Holderied M, McCabe G, Cotton S (2023c) Forest fragmentation and its associated edge-effects reduce tree species diversity, size, and structural diversity in Madagascar's transitional forests. *Biodivers Conserv* 32(10):3329–3353
- Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29(5):773–785
- Hijmans RJ (2023) Raster: Geographic data analysis and modeling. R package version 3.6–26
- Hijmans RJ, Garrett KA, Huaman Z, Zhang DP, Schreuder M, Bonierbale M (2000) Assessing the geographic representativeness of genebank collections: the case of Bolivian wild potatoes. *Conserv Biol* 14(6):1755–1765
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harb Symp Quant Biol* 22:415–427
- Jenkins R, Andriafidison D, Razafimanahaka HJ, Rabearivelo A, Razafindrakoto N, Ratsimandresy Z et al (2007) Not rare, but threatened: the endemic Madagascar flying Fox pteropus Rufus in a fragmented landscape. *Oryx* 41(2):220–228
- Jury MR, Goodman SM, Benstead JP (2022) The climate of Madagascar. In: Goodman SM (ed) *The New Natural History of Madagascar*. Princeton University Press, Oxford, pp 91–99
- Kadmon R, Farber O, Danin A (2004) Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecol Appl* 14(2):401–413
- Kamilar JM, Muldoon KM (2010) The climatic niche diversity of Malagasy primates: a phylogenetic perspective. *PLoS One* 5(6):e11073
- Kass JM (2023) ENMeval: Automated tuning and evaluations of ecological niche models. R package version 2.0.4
- Kemp J, López-Baucells A, Rocha R, Wangenstein OS, Andriatafika Z, Nair A, Cabeza M (2019) Bats as potential suppressors of multiple agricultural pests: a case study from Madagascar. *Agri Ecosyst Environ* 269:88–96
- Kingston T, Vincent Florens FB, Vincenot CE (2021) Crumbling Island keystones: threat diversity and intensification on Islands push large Island fruit bats to the Brink. Preprint *EcoEvoRxiv*
- Kingston T, Vincent Florens FB, Vincenot CE (2023) Large old world fruit bats on the brink of extinction: causes and consequences. *Annu Rev Ecol Syst* 54:237–257
- Kofoky A, Andriafidison D, Ratrimomanarivo F, Razafimanahaka HJ, Rakotondravony D, Racey PA, Jenkins RK (2007) Habitat use, roost selection and conservation of bats in Tsingy de Bemaraha National Park, Madagascar. In: *Vertebrate Conservation and Biodiversity* (Hawksworth, DL. and Bull, AT., Eds.). 213–227. Springer, Dordrecht.
- Kofoky AF, Randrianandrianina F, Russ J, Raharinantenaina I, Cardiff SG, Jenkins RK, Racey PA (2009) Forest bats of Madagascar: results of acoustic surveys. *Acta Chiropterol* 11(2):375–392
- Lang N, Jetz W, Schindler K, Wegner JD (2023) A high-resolution canopy height model of the Earth. *Nat Ecol Evol* 7(11):1778–1789
- Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. *Glob Ecol Biogeogr* 17(2):145–151
- Lučan RK, Bartonička T, Jedlička P, Řeřucha Š, Šálek M, Čížek M et al (2016) Spatial activity and feeding ecology of the endangered northern population of the Egyptian fruit bat (*Rousettus aegyptiacus*). *J Mammal* 97(3):815–822
- MacKenzie DI, Nichols JD, Sutton N, Kawanishi K, Bailey LL (2005) Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* 86:1101–1113
- MacKinnon JL, Hawkins CE, Racey PA (2003) Pteropodidae, fruit bats, Fanihy, Angavo. In: Goodman SM, Benstead JR (eds) *The New Natural History of Madagascar*. University Chicago Press, Chicago, pp 1299–1302
- McDonald MM, Johnson SM, Henry ER, Cunneyworth PM (2019) Differences between ecological niches in northern and southern populations of Angolan black and white colobus monkeys (*Colobus angolensis palliatus* and *C. angolensis sharpei*) throughout Kenya and Tanzania. *Am J Primatol* 81(6):e22975

- Mendes P, Velazco SJE, de Andra AFA, Júnior PDM (2020) Dealing with overprediction in species distribution models: how adding distance constraints can improve model accuracy. *Ecol Model* 431:109180
- Merow C, Smith MJ, Silander JA (2013) A practical guide to maxent for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36(10):1058–1069
- Meyer CF, Struebig MJ, Willig MR (2016) Responses of tropical bats to habitat fragmentation, logging, and deforestation. In: Voigt CC, Kingston T (eds) *Bats in the Anthropocene: conservation of bats in a changing world*. Springer, Cham, pp 63–103
- Morovati M, Karami P, Bahadori Amjās F (2020) Accessing habitat suitability and connectivity for the Westernmost population of Asian black bear (*Ursus thibetanus gedrosianus*, Blanford, 1877) based on climate changes scenarios in Iran. *PLoS One* 15(11):e0242432
- Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for maxent ecological niche models. *Methods Ecol Evol* 5(11):1198–1205
- O'Brien RM (2007) A caution regarding rules of thumb for variance inflation factors. *Qual Quant* 41(5):673–690
- Oleksy R, Racey PA, Jones G (2015) High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascar flying foxes *Pteropus Rufus*. *Glob Ecol Conserv* 3:678–692
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr* 34(1):102–117
- Peterson AT, Papeç M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and maxent. *Ecography* 30(4):550–560
- Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) *Ecological niches and geographic distributions (MPB-49)*. Princeton University Press, New Jersey
- Phillips SJ, Dudík M (2008) Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. *Ecography* 31(2):161–175
- Phillips SJ, Dudík M, Schapire RE (2006) Maxent software for modelling species niches and distributions (Version 3.4.1). Available at: biodiversityinformatics.amnh.org/open_source/maxent/
- Picot M, Jenkins RK, Ramilijaona O, Racey PA, Carriere SM (2007) The feeding ecology of *Eidolon dupreanum* (Pteropodidae) in eastern Madagascar. *Afr J Ecol* 45(4):645
- Potts SG, Ngo HT, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA et al (2016) The assessment report of the intergovernmental Science-Policy platform on biodiversity and ecosystem services on pollinators, pollination and food production Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany. 556pp.
- Racey PA (2016) *Pteropus Rufus*. IUCN Red List Threatened Species 2016:eT18756A22087230
- Racey PA, Goodman SM, Jenkins RKB (2009) *The ecology and conservation of Malagasy bats. Island bats: Evolution, ecology and conservation*. TH Fleming and PA Racey (eds.). conservation of Island bats. University of Chicago Press: 369–405
- Radosavljevic A, Anderson RP (2014) Making better maxent models of species distributions: complexity, overfitting and evaluation. *J Biogeogr* 41(4):629–643
- Rahaingodrahety VN, Andriafidison D, Ratsimbazafy JH, Racey PA, Jenkins RK (2008) Three flying fox (Pteropodidae: *Pteropus rufus*) roosts, three conservation challenges in southeastern Madagascar. *Madagascar Conserv Devel* 3(1):17–22
- Rakotoarivelo AA, Ranaivoson N, Ramilijaona OR, Kofoky AF, Racey PA, Jenkins RKB (2007) Seasonal food habits of five sympatric forest microchiropterans in Western Madagascar. *J Mammal* 88(4):959–966
- Raman S, Shameer TT, Charles B, Sanil R (2020) Habitat suitability model of endangered latidens Salimalii and the probable consequences of global warming. *Trop Ecol* 61(4):570–582
- Ramoni-Perazzi P, Muñoz-Romo M, Chaves LF, Kunz TH (2012) Range prediction for the giant fruit-eating bat, *artibeus amplus* (Phyllostomidae: Stenodermatinae) in South America. *Stud Neotrop Fauna Environ* 47(2):87–103
- Randrianandrianina F, Andriafidison D, Kofoky AF, Ramilijaona O, Ratrimomanarivo F, Racey PA, Jenkins RKB (2006) Habitat use and conservation of bats in rainforest and adjacent human-modified habitats in Eastern Madagascar. *Acta Chiropterol* 8(2):429–437
- Raveloson CO, Andriafidison D, Razafimanahaka JH, Rabesihanaka S, Jenkins RKB (2014) Les baobabs de madagascar: quel cadre réglementaire pour leur conservation? *Madagascar Conserv Dev* 9(1):31
- Raxworthy CJ, Ingram CM, Rabibisoa N, Pearson RG (2007) Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Syst Biol* 56(6):907–923
- Reddy S, Dávalos LM (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *J Biogeogr* 30(11):1719–1727

- Ross LK, Ross RE, Stewart HA, Howell KL (2015) The influence of data resolution on predicted distribution and estimates of extent of current protection of three ‘listed’ deep-sea habitats. *PLoS One* 10(10):e0140061
- Rouse JW, Haas RH, Schell JA, Deering DW (1974) Monitoring vegetation systems in the great plains with ERTS. *NASA Spec Publ* 351:309–317
- Santos H, Juste J, Ibáñez C, Palmeirim JM, Godinho R, Amorim F et al (2014) Influences of ecology and biogeography on shaping the distributions of cryptic species: three Bat Tales in Iberia. *Biol J Linn Soc* 112(1):150–162
- Sattler T, Bontadina F, Hirzel AH, Arletta R (2007) Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. *J Appl Ecol* 44(6):1188–1199
- Scherrer D, Christe P, Guisan A (2019) Modelling bat distributions and diversity in a mountain landscape using focal predictors in ensemble of small models. *Divers Distrib* 25(5):770–782
- Schüßler D, Rabemananjara NR, Radriarimanga T, Rafamantanantsoa SM, Randimbiharirinina RD, Radespiel U, Hending D (2023) Habitat and ecological niche characteristics of the elusive Hairy-eared Dwarf Lemur (*Allocebus trichotis*) with updated occurrence and geographic range data. *Am J Primatol* 85(4):e23473
- Soberón J, Peterson AT (2004) Biodiversity informatics: managing and applying primary biodiversity data. *Philos Trans R Soc Lond B Biol Sci* 359(1444):689–698
- Suzzi-Simmons A (2023) Status of deforestation of Madagascar. *Glob Ecol Conserv* 42:e02389
- Tabarelli M, Peres CA (2002) Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biol Conserv* 106(2):165–176
- Thomas SP (1975) Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. *J Exp Biol* 63(1):273–293
- Thorn JS, Nijman V, Smith D, Nekaris KAI (2009) Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Divers Distrib* 15(2):289–298
- Tran VD, Vu TT, Tran QB, Nguyen TH, Ta TN, Ha TM, Nguyen HV (2018) Predicting suitable distribution for an endemic, rare and threatened species (grey-shanked douc langur, *Pygathrix cinerea* Nadler, 1997) using MaxEnt model. *Appl Ecol Environ Res* 16(2):1275–1291
- van Proosdij AS, Sosef MS, Wieringa JJ, Raes N (2016) Minimum required number of specimen records to develop accurate species distribution models. *Ecography* 39(6):542–552
- Vieilledent G, Grinand C, Rakotomalala FA, Ranaivosoa R, Rakotoarjaona JR, Allnutt TF, Achard F (2018) Combining global tree cover loss data with historical National forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biol Conserv* 222:189–197
- Vogeler AVB, Tschapka M (2021) Effects of land-use on fruit bat distribution in different habitats along the slopes of Mt. Kilimanjaro, Tanzania. *Biotropica* 53(4):1063–1070
- Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc R Soc B Biol Sci* 275(1633):419–425
- Wilmé L, Goodman SM, Ganzhorn JU (2006) Biogeographic evolution of Madagascar’s microendemic biota. *Science* 312(5776):1063–1065
- Wilson DE, Mittermeier RA (2019) Pteropodidae. *Handbook of the Mammals of the World, Vol 9, Bats*. Lynx Edicions, Barcelona, pp 16–162
- Wisn MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, NCEAS Predicting Species Distributions Working Group (2008) Effects of sample size on the performance of species distribution models. *Divers Distrib* 14(5):763–773
- Wunderle Jr. J. M. (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *For Ecol Manage* 99(1–2):223–235
- Zhao XG, Dai W, Li Y, Tian L (2011) Auc-based biomarker ensemble with an application on gene scores predicting low bone mineral density. *Bioinformatics* 27(21):3050–3055