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Predicting current and future distributions of Malagasy bats: Implications for management of coronavirus spillover

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ABSTRACT

Global environmental change is known to be an important factor for the emergence of infectious diseases. Habitat modification of wild animal hosts favor pathogen spillover, particularly in degraded tropical ecosystems. We predicted the distribution of seven of eight bat families on Madagascar in response to climate change and urbanization, based on ecological niche modeling. We found major restructuring of bat-suitable habitats with a large-scale reduction in habitat suitability across all coastal regions of the northern half of the island for all bat families except Molossidae. Indeed, molossid bats follow the anticipated pattern of human population growth and underlines the need for a precise assessment of spillover potential of their associated alpha-coronaviruses.

1. Introduction

Perturbation of habitats where bats occur and aspects of their ecology in response to human land use changes are key drivers of pathogen spillovers [1]. Tropical islands are particularly vulnerable to forest degradation, increased urbanization, invasive alien species, and climate change [2]. In the context of large-scale forest loss, which will result in increased contact between bats and humans, a precise assessment of virus emergence risk on tropical islands is needed, particularly in developing countries having limited health-care systems.

Malagasy forests have been under pressure from agricultural expansion and illegal exploitation of wood resources and this has led over the past 60 years to the loss of approximately 45 % of forest cover [3,4]. Agricultural zones, highly degraded forest, and rural and urban areas have also been colonized by synanthropic mammals, as well as livestock, generating conducive conditions for pathogen spillover. Different forms of contact with bats may also favor zoonotic diseases, in

particular with fruit bats (Pteropodidae) hunted for bush meat and also feeding on fruits consumed by humans, as well as via day-roost sites of insectivorous bats (often Molossidae) in public spaces such as schools, places of worship, and hospitals.

All known human coronaviruses have animal origins and most of them are considered to have originated in bats [5]. Eight bat families containing 46 species are recognized on Madagascar, of which about 80 % are endemic to the island [6]. Bat coronaviruses have been detected on Madagascar, as well as other islands in the western Indian Ocean region, and some of these may be related to viruses of medical importance [7,8]. Herein, we used ecological niche modeling to predict distributions of bat families in response to climate change and urbanization. We then examine how bat family distributions foreshadow coronavirus distribution based on known host-virus associations. Using distribution maps we assess and discuss the current and future viral transmission hazards and the development of spillover risk mitigation strategies on Madagascar.

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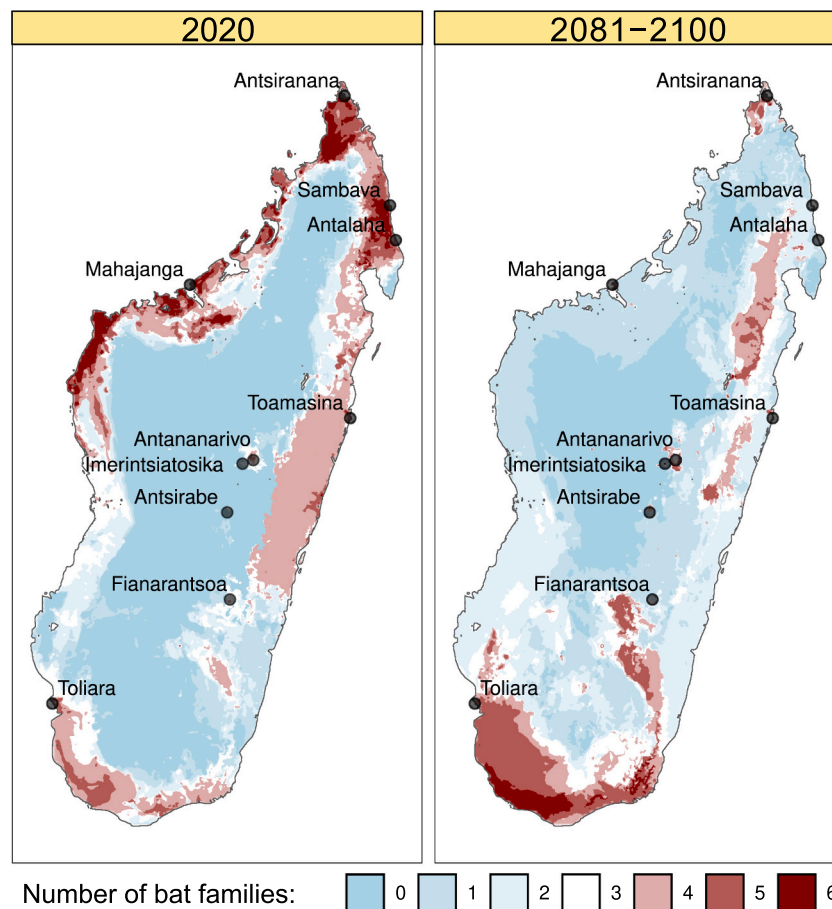


Fig. 1. Malagasy bat family richness (excluding Myzopodidae) and prediction based on worst-case scenario climate models. Areas considered as being suitable habitats for each bat family are defined as geographical areas with statistically above-average model prediction scores (hotspots). The marked cities are those with the 10 highest human populations in Madagascar.

2. Material and methods

A comprehensive database comprising more than 8000 original distributional records of Malagasy bats was employed based on museum specimens and bat surveys up until 2013 [9]. Niche model spatial predictor data combined bioclimatic variables, human population density (as a proxy for the presence of buildings that could act as bat roosts), and limestone distribution for potential cave-roost sites. The use of human population density as a proxy for synanthropic bat roosting is a simplification, as in very high-density urban environments the availability of roosting sites may be reduced due to changes in habitat structure. Nevertheless, this proxy remains appropriate for modeling the general distribution patterns of bat families known to associate with human-modified environments [10,11], particularly given that infrastructure developments associated with the urbanization in Malagasy towns and cities is less pronounced than in developed countries.

All 19 standard bioclimatic variables were downloaded from WorldClim 2.1 (worldclim.org/data/bioclim.html). Human population density (2020) was obtained from Instat Madagascar (2021) and WorldPop (worldpop.org). The distance to exposed limestone, which is associated with the availability of bat cave roosting habitat, was calculated as in Muylaert et al. [12]. This global limestone composite metric calculates the minimum Euclidean distance (km) from these deposits between two data sources: carbonate and evaporite areas from the World Karst Aquifer Map by WHYMAP1 [13] and Open Street Map cave coordinates.

For future predictions (2081–2100), two scenarios were tested: “Middle of the road” and “Worst case”. Middle of the road scenario used

climate prediction (Shared Socioeconomic Pathway 2 with a radiative forcing level of 4.5, i.e. ssp245) from the Canadian Earth System Model v. 5 [14], and human population density predictions (SSP2; [15]). Worst case scenario used climate prediction data for “fossil-fuels” (ssp585) from the Canadian Earth System Model v. 5 [14], and human population density predictions for “fossil-fueled development” (SSP5; [15]). Worst case and Middle of the road scenarios both gave similar spatial prediction trends with different magnitudes of effect. Only Worst case data are presented in this paper.

Ecological niche modeling and projection were performed using the R package ‘ENMTML’ [16]. Point-thinning was performed using the Haversine transformation algorithm based on “cell-size” parameter, which corresponded to a radius of 0.016 degrees (~1.8 km at the equator). Pseudo-absence data was inferred with geographical constraints including only areas further than 50 km from observations. Weighted-mean ensembles were generated using Maxent Simple and Maxent Default maximum entropy algorithms. Predictors were filtered based on collinearity using the Pearson algorithm at a threshold of 0.6. True skill statistics were used to assess model performance, with values >0.6 being considered as “good-fit” and values >0.8 being considered as an “excellent fit”.

All niche model results were processed and visualized in R [17] using the packages “terra” [18], “sf” [19,20], “rgdal” [21], “rgeoda” [22], and “ggplot2” [23]. Areas that were estimated as highly likely to provide suitable habitat conditions for bat families were defined as predictor “hotspots”. Spatial “hotspots” (and “coldspots”) were calculated using the Getis-Ord-G algorithm at a threshold of 1.645, corresponding to the 95 % confidence interval in normally distributed geographic data [24].

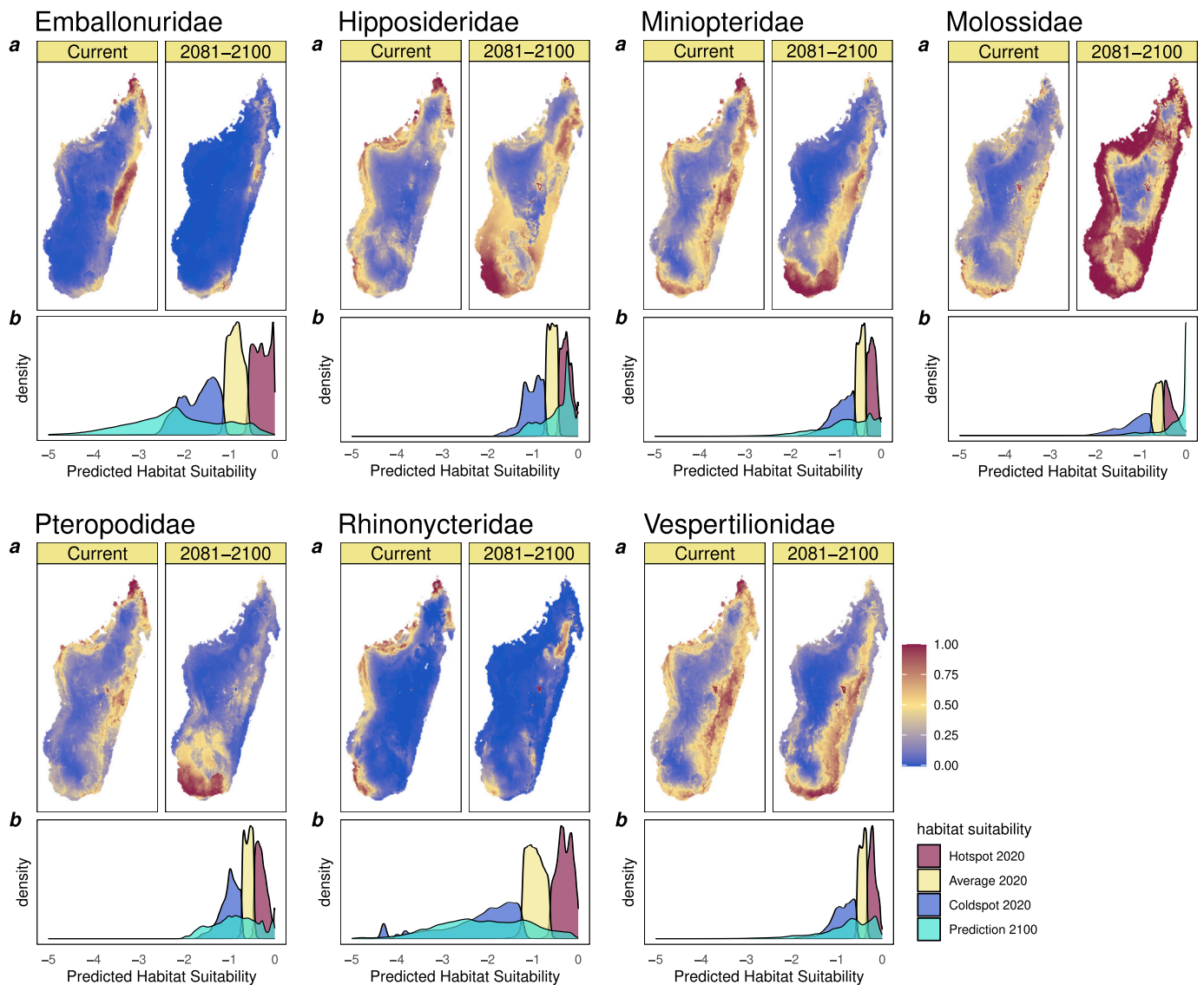


Fig. 2. Predicted habitat suitability for seven Malagasy bat families (excluding Myzopodidae) between 2020 and 2081–2100 based on worst-case scenario climate models. a. Current and future model prediction values, all values fall between 0 and 1. b. Log distribution of spatial model values. Current (2020) model values are divided into statistically below average (coldspot), average and above average (hotspot) habitat suitability values. Future (2081–2100) prediction values are displayed in light blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results and discussion

We generated niche models for seven of the eight Malagasy bat families, excluding the endemic Myzopodidae for which there were too few independent field observations, and an absence of information concerning bat-coronavirus associations. We observed strong collinearity between bioclimatic prediction variables, and retained isothermality, temperature seasonality, temperature annual range, mean temperature of driest quarter, human population density, and distance to cave formations, as predictor layers.

Ensemble niche models performed well for all bat families with true skill statistic scores ranging from 0.61 (good) to 0.85 (excellent). Models predicted a strong influence of factors relating to temperature, with low temperature variability strongly favorable for the following families: Emballonuridae, Miniopteridae, and Vespertilionidae (insectivores), and Pteropodidae (frugivores). Conversely, higher temperatures in dry seasons were favorable to the insectivorous families Hipposideridae and Rhinonycteridae. As expected, shorter distances to limestone formations had a positive effect for bat families comprising cave-dwelling species; higher human population densities favored families with synanthropic

species, most notably Molossidae.

Climate change projections for 2081–2100 revealed a dramatic restructuring of suitable habitats and their distributions for all bat families, with a large-scale reduction across all coastal regions of the northern half of Madagascar, with the exception of Molossidae (Figs. 1 and 2). In addition, the amount of suitable habitat for members of this family may notably increase across all of Madagascar, and contrasts with the reduced distribution of the other six families (Fig. 2).

The ancient coevolutionary relationships between bats and their associated alpha- and beta-coronaviruses [25,26] has shaped the diversity and geographical distribution of bat coronaviruses, which are driven by variation in the biogeography of bat hosts [27]. Predicting spatial hazards associated with public health of bat-borne coronaviruses may thus be feasible by modeling changes in host distribution driven by habitat and climate shifts. This strong host specificity, combined with the growing availability of molecular data, provides a unique opportunity to assess zoonotic risk in a spatially explicit manner.

This predictive framework may also be applicable to other bat-borne infectious agents for which some level of host specificity has been described (e.g. *Leptospira* spp. [28]). However, it cannot be generalized

across all infectious agents due to weaker host associations or limited knowledge on host range and interspecies transmission ([29] for a review). In addition, other parameters should also be considered for foreseeing and controlling virus emergence, which include virological factors (e.g. pre-adaptation to new host receptors, recombination) and socio-demographic characteristics of the human population. Although our modeling exercise does not include such parameters, our results nevertheless suggest major shifts in the distribution of bat families on Madagascar and in turn their associated viruses.

Bat families that will undergo significant changes in their geographic distributions should be the subject of further epidemiological surveillance. For example, coronaviruses known from hipposiderid bats are potentially highly diverse (Duvinacovirus, Setracovirus, Sarbecovirus, and Hibecovirus) and may include viruses of medical importance (closely related to Human coronavirus 229E, NL63, and SARS). Beta-coronaviruses have been detected in Malagasy Pteropodidae [7,8], for which spillover risk may be associated with hunting and bush meat consumption. Finally, alpha-coronaviruses associated with the Molossidae are closely related to those detected in other bat species on western Indian Ocean islands [8], such as on La Réunion, where annual prevalence in bats can reach up to 80 % [30]. For Madagascar, we found that the distribution of Molossidae follows shifts in human demography, and therefore calls for a precise assessment of spillover potential of these bats associated alpha-coronaviruses.

Beyond their role as reservoirs of infectious agents with zoonotic potential, Malagasy bats provide essential ecosystem services that support both biodiversity and human well-being. Frugivorous species contribute to seed dispersal and forest regeneration, facilitating the maintenance of native plant communities, while insectivorous bats (e.g. Vespertilionidae, Molossidae) play a key role in regulating insect populations, including agricultural pests [31]. Major changes in bat distribution associated with changes in climate and land-use will likely impact not only ecosystem functioning but also the resilience of socio-ecological systems. In this context, protecting bat populations is not only a matter of public health but also a priority for biodiversity conservation, human well-being, and the sustainability of ecosystem services across Madagascar's threatened natural landscapes.

Finally, although our study highlights major spatial shifts in bat family distributions and their potential implications for zoonotic risk, it does not explore the regional-scale ecological or socio-political factors that may mediate these risks. Madagascar harbors seven major ecoregions, a large diversity of micro-habitats and nearly 80 % of its bat species are endemic to the island, making species-level and locally contextualized analyses highly complex. Patterns of ecological change across Malagasy ecoregions are highly variable and are influenced by a complex interplay of socio-economic and political factors [3]. Such heterogeneity is particularly challenging to integrate into predictive models, given the diversity of socio-cultural and ecological contexts across this island nation.

Declaration of AI use

We have not used AI-assisted technologies in creating this article.

CRedit authorship contribution statement

Riana V. Ramanantsalama: Writing – original draft, Conceptualization, Investigation, Formal analysis. **David A. Wilkinson:** Writing – original draft, Investigation, Formal analysis. **Renata L. Muylaert:** Writing – review & editing, Methodology, Investigation. **Steven M. Goodman:** Data curation, Writing – review & editing, Investigation, Resources. **Camille Lebarbenchon:** Writing – original draft, Conceptualization, Investigation, Funding acquisition.

Ethics

This work did not require ethical approval from a human subject or animal welfare committee.

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Declaration of competing interest

We declare we have no competing interests.

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Data availability

Data will be made available on request.

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