Temporal matching of occurrence localities and forest cover data helps improve range estimates and predict climate change vulnerabilities

Original Research Article

Temporal matching of occurrence localities and forest cover data helps improve range estimates and predict climate change vulnerabilities

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ABSTRACT

Improved quantification of species' ranges is needed to provide more accurate estimates of extinction risks for conservation planning. Highland tropical biodiversity may be particularly vulnerable to the anthropogenic changes in land cover and climate and is subject to over-estimation of geographic range size in IUCN assessments. Here, we demonstrate a novel and practical approach for quantifying inferred range reductions based upon temporal matching of recent species occurrence localities and vegetation data. As an illustration pertinent to montane forest-associated species with limited distribution data, we use *Gymnuromys roberti*, an endemic Malagasy rodent with a Least Concern conservation status. We estimated climatic suitability and climate change vulnerability using species distribution modeling (SDM). We then determined deforestation tolerance thresholds for the species by temporally matching recent occurrence localities with percent forest cover values from MODIS forest cover layers. Finally, we applied these thresholds in postprocessing SDM-based range estimates. These estimates demonstrate that the lack of sufficient forest cover substantially reduces the species' current estimated range compared with the IUCN range map. Projections to 2050 suggest that there will be a loss of climatic suitability over three quarters of the currently suitable habitat along with increased fragmentation, highlighting the need to include climate change vulnerability assessments as an integral part of conservation planning. Broader application of SDMs could assist practitioners at various stages of conservation planning, stressing the need for improved accessibility of methodologically complex SDM approaches.

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1. Introduction

Global biodiversity is rapidly declining due to anthropogenic habitat disturbances exacerbated by ongoing climate change (Urban, 2015; Johnson et al., 2017). These declines are especially pronounced in biodiversity hotspots, where assemblages of high species richness and endemism suffer significant habitat loss due to land cover change (Myers et al., 2000). Many of these hotspots are found in tropical montane regions (Jenkins et al., 2013), and highland tropical biodiversity may be particularly susceptible to the threat of habitat loss compounded by climate change (La Sorte and Jetz, 2010). While montane topography presents opportunities for upslope range shifts as species track their climatic niches, many taxa with low dispersal abilities, narrow elevational ranges or little upslope space to occupy are expected to face increased extirpation risks (McCain and Colwell, 2011). The potential for range shifts is further restricted by natural fragmentation of montane landscapes due to environmental heterogeneity and topographic barriers. Such natural fragmentation is further exacerbated by anthropogenic disturbances, such as deforestation. In a climate-change context, low connectivity makes isolated areas of suitable habitat unavailable for colonization even if they become larger or more suitable.

Therefore, worldwide, but especially in tropical montane regions, there is considerable need to address biodiversity declines. The situation also calls for implementation of effective conservation strategies that account for uncertainty due to changing environmental conditions (Hannah et al., 2007; Araújo et al., 2011). Decisions regarding land use and sustainable management of species' habitats are a crucial component of conservation efforts, and actions to prioritize areas for protection are often based on species-specific and systematic conservation assessments (Rodrigues, 2011). Globally, the International Union for Conservation of Nature (IUCN) uses such assessments to classify species based on levels of extinction threat according to several criteria related to the range size and quality of habitat, as well as population size and structure (IUCN, 2012). IUCN recognizes three threatened categories (Critically Endangered, Endangered, and Vulnerable) and two non-threatened categories (Near Threatened and Least Concern, or LC). Species with insufficient information for an assessment are assigned a data-deficient category, which includes many poorly known small mammals. However, an assessment does not have to include all IUCN criteria. For taxa without sufficient population data – which is often the case for tropical species, ranging from plants to both invertebrates and vertebrates – knowledge about available habitat can be used to assess conservation status based on criterion B (geographic range size). IUCN protocols for criterion B provide thresholds that must be met for various risk categories based on either Extent of Occurrence (EOO; area of the polygon around known occurrence localities) or Area of Occupancy (AOO; area occupied by the species).

While the IUCN criteria were designed to address threats for a broad range of taxa objectively, revisions and improved approaches are continually proposed. These include ways to evaluate risks based on remaining area of habitat (AOH) as an estimate of the upper bounds of AOO (Ocampo-Peñuela et al., 2016; Brooks et al., 2019). After the generalized IUCN geographic range maps (usually drawn in a coarse manner based on comments from experts) are revised with species' elevational limits, habitat associations, and land cover data, ample studies demonstrate that many species are at a greater extinction risk than their current conservation status suggests (Harris and Pimm, 2008; Beresford et al., 2011; Li et al., 2016; Ocampo-Peñuela et al., 2016). Overestimation of geographic range sizes is particularly prevalent in montane regions (Harris and Pimm, 2008), where many endemic species already have naturally limited and fragmented ranges. Furthermore, even protected areas that harbor suitable habitat within realistically refined species' ranges may become less adequate in the future, as species shift in elevation in response to altered environmental conditions (Hannah et al., 2007; Araújo et al., 2011; Alagador et al., 2014). Although simulations show that the IUCN system of risk assessment is adequate under climate change with regularly updated species evaluations, the warning time to extinction after the initial listing of a species in a threatened category is substantially shorter when assessments are made using a single risk criterion (Stanton et al., 2015). Thus, the situation for species with limited data, where by necessity assessments are generally based on a single criterion (geographic range size), may leave a narrower temporal window for conservation action. This creates a potential for rapid deterioration of IUCN risk category with subsequent reassessments, leading to the need for approaches that harness recent environmental data to facilitate frequent assessments for such species.

1.1. Approaches to estimating range size

Although accurate estimates of species distributions are essential for conservation planning to be effective, various obstacles have limited the production of realistic estimates of current and future ranges. Improved access to biodiversity data (i.e., species occurrences) as well as environmental variables (i.e., climate, land cover, soils) has fueled a proliferation of species distribution-based conservation studies ranging from the investigation of individual species' risks to identification of regional and global conservation priority areas (Anderson and Martínez-Meyer, 2004; Jenkins et al., 2013; Li et al., 2016; Gerstner et al., 2018). Common methodologies for estimating species' distributions often rely on expert range maps or correlative modeling of species' environmental associations, which provide geographic estimates of the areas suitable for the taxa at hand. Generalized range maps are informed by expert knowledge about species' occurrences and habitat associations, but they often overestimate the true geographic range and may not be available for data-poor or rare species (Hurlbert and Jetz, 2007; Peterson et al., 2016; Pimm et al., 2017). They can be used to estimate upper bounds of EOO and AOO but still rely on expert knowledge regarding coarse habitat associations. In contrast, correlative species distribution models (SDMs) infer species' environmental associations from species occurrence data and environmental conditions at those localities; the range predictions that such models provide are also typically overestimates, especially given that they are usually based only on long-term environmental data (especially

regarding climate; Peterson et al., 2011). SDM projections can estimate suitable areas and thus provide range predictions for species that lack range maps, but they require careful consideration of model assumptions (Araújo and Peterson, 2012; Yackulic et al., 2013); modeling algorithm selection (Elith et al., 2006, 2010); model parameters, evaluation, and selection (Warren et al., 2014; Galante et al., 2018); sampling bias (Anderson and Raza, 2010; Boria et al., 2014; Warren et al., 2014); biotic interactions (Kass et al., 2021); and other important issues (Araújo et al., 2019). Both the range map and the SDM approaches would benefit from consideration of various kinds of current land cover data, with species' tolerances informed using recent occurrence data. However, vegetational data seldom are used as predictor variables in SDMs, because the vast proportion of available occurrence records typically come from museum collections predating remotely sensed data.

To help fill this void, we propose a simple, practical data-driven way to use recent occurrence localities and land cover information to improve estimates of species' current distributions, applicable for post-processing of range estimates from either expert range maps or SDM predictions. We provide a worked example pertinent to conservation of species with limited data currently deemed non-threatened in a time of global change (Fig. 1), using an endemic montane Malagasy rodent species, *Gymnuromys roberti*, categorized as Least Concern. In doing so, we do not intend for the results to be used in guiding conservation applications for this species per se (e.g., by following all recommendations in Araújo et al., 2019; IUCN, 2019); rather, we aim to provide an intuitive demonstration of a general methodology applicable to enhancing the process of IUCN risk assessment using the criterion of geographic range size. We first estimate climatic suitability in the SDM framework to benefit from its applicability to forecast shifts in species distributions due to climate change (Anderson, 2013). We then use recent occurrence locality data and remotely sensed landcover data to elucidate the species' vegetational tolerances; specifically, we employ a novel yet simple approach of temporally matching recent occurrence localities to forest cover information (although any relevant variable reflecting vegetation could be used). Next, we use the resulting estimate of vegetational tolerances to postprocess the SDM output, yielding an estimate of the species' current range. Finally, we quantify the areal extent of that prediction and consider maps of current protected areas (PAs) as an example of how such information can be used to analyze the adequacy of present IUCN listings and current conservation strategies.
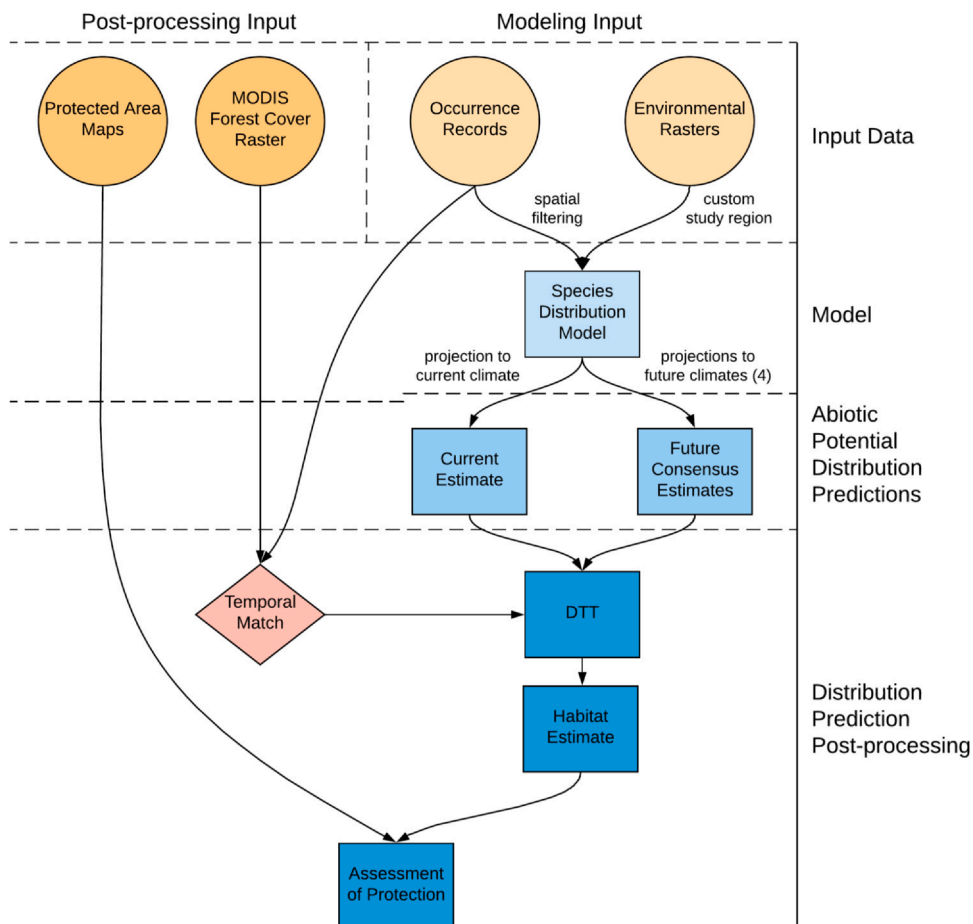
Fig. 1. Flowchart illustrating the methodology used, including the proposed use of temporal matching of recent occurrence records and remotely sensed land cover information to determine habitat associations (here, a deforestation tolerance threshold for *Gymnuromys roberti*).

2. Methods

2.1. Study system

To demonstrate the utility of the proposed approach for montane tropical species in regions of conservation concern, we focus on Madagascar, a biodiversity hotspot with high levels of biodiversity and endemism for which the future existence of numerous plant and animal species is threatened by rapid deforestation (Myers et al., 2000; Jenkins et al., 2013; Goodman et al., 2018). Over 90% of the Malagasy biota is unique to the island, with many taxonomic groups experiencing a considerable increase in diversity estimates in recent years due to ongoing biological survey efforts and concerted taxonomic research (Goodman and Benstead, 2005; Goodman et al., 2018). However, anthropogenic land uses such as mining, illegal logging, and slash-and-burn agriculture have severely reduced and fragmented the island's natural forests (Harper et al., 2007; Styger et al., 2007, Vieilledent et al., 2018), making the prioritization of conservation efforts critical. Moreover, Madagascar has a high concentration of endemic mammals with naturally small ranges, many of which are currently listed as non-threatened by IUCN (Jenkins et al., 2013). Although current range sizes may not place a species in a threatened IUCN category, future reduction in range size due to habitat loss and climate change may put portions of the Malagasy biota at risk of higher extinction rates in the next decades. These aspects make Madagascar an area where SDM-based prognoses of future risk can advance conservation planning. The PA coverage in Madagascar has expanded rapidly in recent years (Gardner et al., 2018; Goodman et al., 2018), with the design of the PA network informed by systematic conservation assessments based on SDMs for multiple species across several taxonomic groups (Kremen et al., 2008; Guisan et al., 2013). The island's current PA system includes both strict (IUCN categories I, II and IV) and multiple-use (IUCN categories III, V and VI) PAs where extractive resource use is legally allowed (Goodman et al., 2018); the network continues expanding with newly proposed sites as well as temporary PAs with mining moratoriums seeking permanent PA status (Gardner et al., 2018). The near future is likely to present a test of robustness of the island's PA system to the combined effects of changes in land cover and climate, which are projected to cause shifts in biodiversity patterns across the island, particularly in the vulnerable Central Highlands and eastern moist evergreen forest ecoregions (La Sorte and Jetz, 2010; Brown et al., 2015).

2.2. Study species

We implement the proposed methodology with *Gymnuromys roberti*, as an example pertinent to other species currently considered non-threatened, and, hence, overlooked in conservation planning despite potential vulnerability to several risk factors. This monospecific genus belonging to the Malagasy endemic rodent subfamily Nesomyinae is broadly distributed in medium altitude moist evergreen forest in the eastern and northern portions of the island (500–1625 m elevation; Goodman et al., 2013). Few details are known about its natural history and ecology, but it is forest-dwelling and infrequently captured during small mammal inventories as compared to most other genera of nesomyine rodents (Carleton and Goodman, 2003; Soarimalala and Goodman, 2011). *Gymnuromys roberti* has been trapped at a few sites with secondary native forest and introduced tree species, including eucalyptus plantations; hence, it seems tolerant to certain levels of habitat disturbance and deforestation (Carleton and Goodman, 2003). Due to its broad geographic range and presence within several PAs, the species is currently categorized as LC by the IUCN (Kennerley, 2016). However, the moist evergreen forest inhabited by the rodent is fragmented and under the influence of continued deforestation despite the establishment of several PAs (Grinand et al., 2013).

2.3. Occurrence data

Occurrence data for *G. roberti* were compiled from museum records (48 unique localities; Table S1), most based on fieldwork over the past three decades and used to derive the range map in Goodman et al. (2013). To alleviate the effects of sampling bias typical of such datasets, we spatially thinned the locality dataset using the R package spThin (Aiello-Lammens et al., 2015) with a thinning distance of 10 km following a previous study on a widespread montane small mammal species in moist evergreen forest in Madagascar (Boria et al., 2014).

2.4. Environmental data

For the current and future environmental data, we used 19 bioclimatic variables from worldclim.org (30″ resolution; Hijmans et al., 2005). Georeferencing of localities without GPS coordinates (specifically, the older ones) is unlikely to be accurate enough for association with finer grains. Little is known regarding the natural history of *G. roberti*, but these variables represent ecologically plausible limiting factors for the species and have been used successfully to predict ranges of other small mammals in the region (Boria et al., 2014, 2017). Under the classifications of Austin (2002), they plausibly represent direct variables that affect organisms physiologically but are not consumed by them, although we note that they would be distal (only linked to the proximal ones that determine the species' physiological response; see also Austin and Van Niel, 2011; Anderson, 2013). However, as is common for so many tropical species, limited knowledge about the natural history of *G. roberti* limits efforts to pinpoint the particular variables most relevant for these models. Fortunately, the use of regularization by Maxent (see below) facilitates a machine-learning selection among ecologically plausible predictor variables. The future environmental data were the climatic estimates used in the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2013). We

used climatic estimates based on two General Circulation Models (GCMs) for two Representative Concentration Pathways (RCPs) for the year 2050. Uncertainties introduced by different GCMs and RCPs result in variation in the geographic predictions from SDMs, and considering several GCMs and RCPs has been suggested to encompass the breadth of future climatic suitability (Goberville et al., 2015). In this study, we used two GCMs (MIROC5 and CCSM4) and selected two emission scenarios (high emission RCP 8.5 and medium-range emission RCP 6.0) expected to produce higher risk for the species and thus lead to greater conservation concern, hence representing an upper bound of the uncertainty regarding emissions.

2.5. Study region

For model calibration, we delineated a custom study region to exclude peripheral geographic areas with no known occurrence records of *G. roberti*, possibly unoccupied due to dispersal barriers or biotic interactions, or occupied but insufficiently sampled (Peterson et al., 2011). The extent of the study region is known to affect SDM predictions and should be selected to reflect environmental conditions available through dispersal (Anderson and Raza, 2010; Barve et al., 2011; Barbet-Massin et al., 2012). As the few known occurrences of the species are broadly distributed in a relatively narrow strip within an environmentally heterogenous montane region, we restricted the background (randomly selected 10,000 points) by creating a circular 0.7° buffer around each locality of the spatially thinned occurrence dataset.

2.6. Modeling

We made a prediction of suitability as a vehicle for illustrating the relevance of our data-driven post-processing. In building this SDM, postprocessing it, and examining its projections into the future, we minimized some sources of uncertainty (e.g., by using highly vetted occurrence data) and addressed variation associated with other issues particularly relevant to understanding the use of the postprocessing approach. For studies intended for biodiversity assessments, we suggest a fuller characterization of the effects that decisions made regarding modeling methods may have on the variation in the final suitability predictions (for example, via consideration of additional algorithms; Araújo et al., 2019). Here, we followed SDM practices suitable for a species with few occurrence records that allow for characterizing variation in model predictions and estimating optimal model complexity (see below for additional consideration of uncertainty related to deforestation tolerance thresholds, GCMs, and RCPs). We built SDMs and tuned their settings using Maxent 3.3.3k, a high-performing algorithm that predicts environmental suitability for a species by comparing environmental data values at occurrence localities with those sampled from the background of the study region (Elith et al., 2006; Phillips et al., 2006). Because Maxent models vary substantially according to the settings employed regarding feature classes and regularization multipliers (Merow et al., 2013; Radosavljevic and Anderson, 2014), we explored inter-model variation and estimated optimal model complexity with a tuning exercise using the R package ENMeval (Muscarella et al., 2014). This resulted in 32 candidate models spanning a wide range of complexities and evaluating their performance on withheld data using an *n* - 1 jackknife approach (Pearson et al., 2007; Shcheglovitova and Anderson, 2013). We selected the optimal model settings using sequential criteria of lowest average test omission rate based on the minimum training presence threshold (greater predictive ability) followed by highest test AUC (greater discriminatory ability) and used these settings to generate the final suitability prediction (Shcheglovitova and Anderson, 2013).

2.7. Spatial projections

To estimate which areas were climatically suitable for the species, we projected the optimal model onto geographic space using current and future climatic variables over the entire island. This yielded one current and four future suitability maps, which we then converted to binary predictions using the minimum training presence threshold (to indicate suitable vs. unsuitable areas). We stacked the four predictions of future suitability (RCP6.0-CCSM4, RCP6.0-MIROC5, RCP8.5-CCSM4, RCP8.5-MIROC5) to estimate variability in geographic predictions. The areas that were predicted as suitable by all four future climate scenarios constituted the most conservative consensus estimate.

2.8. Forest cover

We then processed both present and future abiotic suitability predictions using forest cover data to account for the species' habitat associations. To examine the quality of habitat associated with *G. roberti*, we used MODIS Vegetation Continuous Fields (VCF) for the years 2000–2010 at a 250 m spatial resolution – relatively coarse for land cover datasets (DiMiceli et al., 2011). MODIS VCF datasets provide estimates for heterogeneous land cover (tree cover, non-tree cover, non-vegetated), with a percent forest cover value assigned to each cell. We extracted percent forest cover values at each of the most recent occurrence localities (collected in the years 2000–2010) with high quality georeferences (GPS coordinates; *n* = 32; Table S1), using the respective forest cover layers matched to the year of specimen collection. Such temporal matching allowed us to characterize the amount of forest remaining in the respective grid cell when the species was collected.

We then used these percent forest cover values to define a 'deforestation tolerance threshold' (DTT). Categorizing 'forest' is difficult, because definitions are often based on arbitrary percent tree cover thresholds; this leads to discrepancies in geographic estimates of forest cover, especially in tropical biomes with intermediate forest cover such as Madagascar (Sexton et al., 2016). In such situations, use of a forest cover dataset at a coarser grain is more informative than finer-grain data, as it allows to better

describe the overall local conditions and evaluate habitat associations. For example, capture of a specimen traversing a 30 by 30 m pixel lacking tree cover may be falsely interpreted as a species' ability to persist in such conditions, whereas a tree cover value from a 250 by 250 m pixel would be more representative of the forest quality in the vicinity of the specimen's capture, reflective of what the animal experiences throughout its home range. Here, rather than applying one of the standard forest cover criteria (> 10%, from > 10% to > 30%, or > 60%), we implemented a species-specific approach to define the minimum DTT as the lowest percent forest cover value at known occurrence localities. However, from occurrence data alone we could not rule out a possibility that some specimens may have been collected in areas of recent deforestation, where the species had not yet reached equilibrium with the modified environment, i.e., sink populations doomed to extirpation (Grainger, 1999). Additional uncertainty was introduced by the use of a relatively coarse MODIS dataset with limited knowledge about the natural history of the species (i.e., unknown individual home range size vs. grain of the environmental data). Recognizing these concerns, we also identified a second, more conservative threshold expected to encompass higher quality habitat with less disturbance. We did so by removing data points presumed to be outliers, which corresponded to the 10% of localities with the lowest forest cover values.

To estimate the extent of available habitat, we then masked the most recent MODIS forest cover layer (thresholded by the minimum and conservative DTTs, respectively), by each of the binary SDM predictions. First, we applied the minimum and the conservative DTTs to the most recent (2010) MODIS layer to produce two binary maps, each of which we then masked by a binary SDM prediction corresponding to present climatic conditions. We compared the two DTT-informed estimates of presently available habitat with the IUCN range map by stacking the layers and calculating overlap. Then, for future habitat estimates, we used SDM predictions for 2050 to mask the 2010 forest cover layer thresholded by the conservative DTT only. This latter processing assumes static forest cover (no loss or gain of forest cover between 2010 and 2050). We calculated range areas under different forest cover thresholds at present and in the future from the resulting maps, yielding estimates analogous to AOH but derived from data-driven approaches (SDM postprocessed using DTT). However, as both AOH and our quantifications represent estimates of the upper bound of Area of Occupancy (AOO; Kass et al., 2021), we compared our results to IUCN's cutoffs for that measure (although note that for strict comparison AOO values should normally be calculated on a 2 × 2 km grid). We then conducted an analysis of PA coverage using maps of established PAs as of 2018 (UNEP-WCMC) to quantify how much of the species' predicted range is within the national PA system and to determine if areas of primary concern for the species are adequately targeted by conservation strategies.

3. Results

3.1. Current climatic suitability

The estimated climatically suitable area for *G. roberti* extended from north to south along the eastern portion of the island in a fragmented band of variable width (model H-1.5 in Table S2; Fig. S1). Several extensive environmentally suitable areas tapered to corridors constricted by unsuitable conditions, with a narrow disjunction between the northern and central parts of the prediction. Notably, the area immediately to the north of the disjunction, within the Mandritsara and Andilamena districts, was predicted as suitable but did not have any known occurrence records for the species, likely due to the lack of biological inventories in these zones (Goodman et al., 2013, Fig. 1).

3.2. Forest cover

We determined two moderately different forest-cover thresholds that considerably restricted the climatic suitability estimate, resulting in an estimate of habitat extent similar to that of the IUCN range map (Fig. S2). The minimum DTT corresponded to 18% forest cover and the conservative DTT to 40% forest cover. Removal of areas lacking the necessary forest cover exacerbated the natural fragmentation observed in the SDM prediction. Application of the minimum DTT showed that slightly more than half of the SDM-predicted range (55%) had enough forest cover to support the species (Fig. 2). However, the conservative DTT indicated that forested areas with lower levels of disturbance constituted a substantially smaller area (39% of the SDM prediction). Masking this latter projection by PA boundaries demonstrated that only 19% of the SDM prediction was sufficiently forested and presently protected (Figs. 2-3). The IUCN range map (a smooth continuous polygon) was in good agreement with the outline of the SDM prediction masked by either of the two DTTs (Fig. S2). However, the range map did not reflect the fragmentation of suitable habitat along the edges and the northern and southern portions of the range, resulting in a greater range estimate than our analyses. With the minimum DTT threshold, only 64% of the IUCN range map was predicted as suitable, decreasing to 47% with the conservative DTT. Moreover, the range map excluded a substantial area in the north predicted as suitable by the masked SDM (Bemanevika, Mahimborondro, and Tsaratanàna PAs; PAs 1–3 in Fig. 3), albeit without known occurrence records (specifically, 18% and 16% of the forested SDM range prediction was outside the IUCN range map boundaries with the minimum and the conservative DTTs, respectively).

3.3. Future suitability

SDM predictions for 2050 varied moderately among the four future projections and were affected by both GCM and RCP choice (Figs. 2, S3, S4). Projections based on RCP 8.5 predicted a greater decrease in climatically suitable area than those based
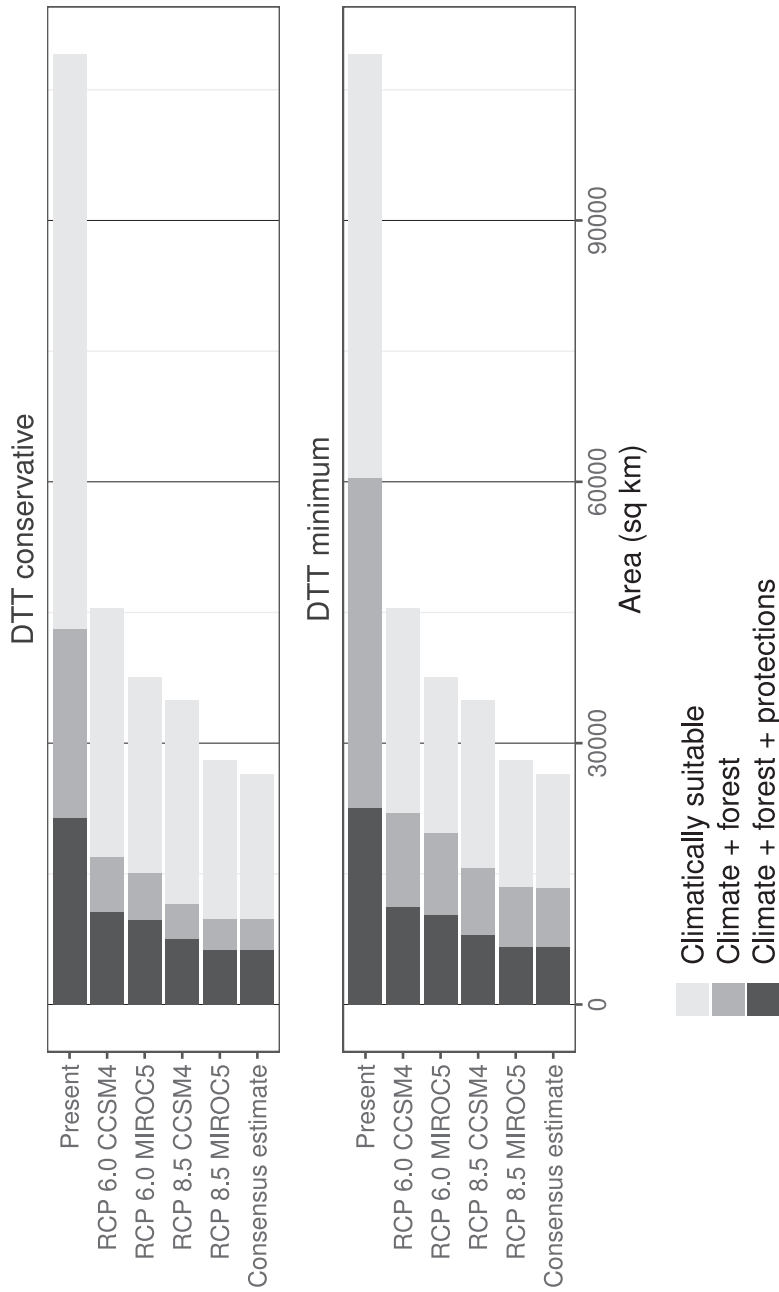
Fig. 2. Areal estimates (km^2) of present and future (year 2050) climatic suitability, forest cover, and protection status for *Gymnuromys roberti* on Madagascar. Estimates were calculated under the minimum deforestation tolerance threshold (min DTT, 18% forest cover; bottom panel) and the conservative DTT (40% forest cover; top panel). Future projections estimate suitability under four models of projected climate in 2050. Areas predicted as suitable by all four future estimates constitute the consensus estimate.
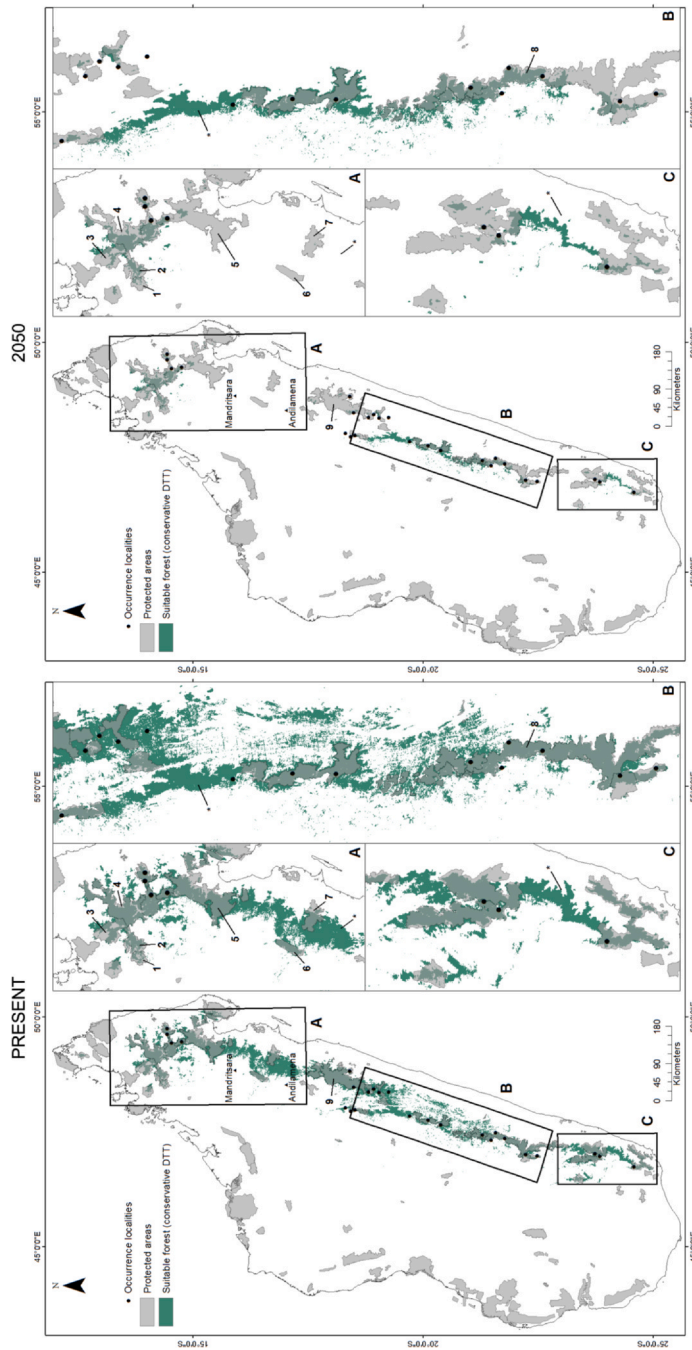
Fig. 3. Level of habitat protection for *Gymnuromys roberti* on Madagascar at present (left panel) and in 2050 (right panel). Areas shown in green are estimated to be suitable climatically (currently, left; consensus estimate for 2050, right) and are forested above the conservative deforestation tolerance threshold (conservative DTT, 40%; MODIS forest cover layer from 2010). Polygons show existing protected areas (PAs). Northern (inset A), southern (inset C) and middle (inset B) parts of the range are shown in greater detail with some of the PAs labeled as follows: 1 – Bemanevika; 2 - Mahimborondro; 3 – Tsaratanàna; 4 – Ambohimirahavavy; 5 – Makira; 6 – Marotandrano; 7 – Ambatovaky; 8 – Ambositra-Vondrozo. Stars denote extensive tracts of presently suitable habitat outside of PA borders. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

on RCP 6.0. Similarly, estimates based on MIROC5 were more restrictive than those from CCSM4. Despite the variability in areal estimates, all future predictions forecast smaller range areas than those based on present climate, and those areas were further restricted by forest cover. SDM predictions for 2050 ranged from 42% (RCP6.0-CCSM4) to 26% (RCP8.5-MIROC5) of the present SDM prediction (Fig. 2). The consensus estimate, encompassing areas suitable according to all four future SDM predictions, constituted only 24% of the present SDM estimate, and less than half of this consensus estimate was forested above the conservative DTT ($9800 \, km^2$). This estimate exceeded the IUCN criterion B (area of occupancy less than $2000 \, km^2$) for the Vulnerable extinction risk category both at present and in the year 2050. While this currently widespread species would remain in LC category at present by the upper-bound estimates produced by our approach, the future estimates suggest that it is likely to qualify for a Near Threatened listing by 2050.

3.4. PA coverage

Our assessment of the protection status of the species' habitat showed that large areas with high climatic suitability and adequate forest cover were encompassed by Madagascar's PA system for both the current and future predictions (Figs. 2–3). Current PAs covered nearly two thirds of the forested consensus estimate for 2050 ($6000 \, km^2$ out of $9700 \, km^2$). The PA network in the north (PAs 1–5; Fig. 3) covered most of the sufficiently forested consensus prediction for 2050 in that region, although *G. roberti* has not been recorded in several of those PAs and in certain cases no small mammal inventories have been conducted there. Importantly, we identified large tracts of suitable habitat predicted to remain climatically suitable in the future that currently lack protection (indicated by stars in inserts B and C in Fig. 3). We also found several PAs as well as suitable unprotected areas that could lose all climatic suitability by 2050 (PAs 5–7 and 9, starred area in insert A; Fig. 3).

4. Discussion

This study is an example of a simple data-driven analysis that can be used to estimate extinction risk and gauge the robustness of conservation planning for species that may be particularly vulnerable to land use change and climate change, such as tropical montane biota. The extent of suitable remaining habitat derived from combined SDM-DTT approach was similar to the IUCN range map, albeit with several discrepancies that would require additional field work to determine if the species is present in the areas of disagreement. We demonstrate that a carefully built SDM with data-driven postprocessing to consider land cover is a valuable resource that can be used instead of, or in concert with, expert-driven range maps to inform conservation efforts. Additionally, the SDMs allowed explicit estimation of future risks. The magnitude of the projected decrease in the extent of habitat along with an increase in fragmentation within the next three decades is an alarming forecast, especially because such vulnerability to climate change may be overlooked in species listed as LC. This study underscores the need to include climate change vulnerability assessments, such as this distributional trend prognosis, as a routine step of formal IUCN assessments to better mediate the effects of climate change for species with a projected decrease in habitat suitability (Foden et al., 2019).

4.1. Current suitability

Qualitative analysis of the present abiotic SDM-based prediction identified several large, contiguous areas of high suitability, some of which were severely reduced when we applied the two forest cover thresholds. Natural fragmentation compounded by deforestation led to substantial breaks in habitat connectivity. On the basis of available data, the current range of *G. roberti* holds several large but nearly disjunct tracts of suitable habitat connected only by narrow corridors, suggesting the existence of isolated populations (Goodman et al., 2013). Additional sampling in suitable areas that currently lack occurrence records is almost certain to uncover yet unknown *G. roberti* populations. As a complement to the SDM approach, genetic analyses are needed to characterize the phylogeographic relationships and discover any genetic differentiation among populations of this widely distributed species, as has been documented in another genus of nesomyine rodent (Jansa et al., 2008). If disjunct localized populations in distinct montane regions are sufficiently differentiated, *G. roberti* as currently recognized may actually be a complex of several species or subspecies that merit individual conservation consideration. If that is indeed the case, the ranges of constituent entities would be much smaller than the estimates presented here, leading to higher levels of risk and perhaps a vastly different conservation status.

4.2. Future suitability

The analysis of future abiotic suitability based on scenarios of short-term climate change revealed that habitat loss due to current deforestation would likely be exacerbated in the future. This highlights the relevance of both a carefully applied SDM approach (allowing model transfer across time) and the DTT methodology for improving IUCN assessments of species' risks, especially in data limited cases based on range size estimation alone. All four future projections predicted a substantial decrease in the extent of suitable areas, especially in the northern and southern parts of the range. Even with the optimistic assumption that forest cover remains static over the next few decades, the predicted decrease in suitable habitat could cause further isolation of populations. The consensus estimate (where all four projections agree) combined with the conservative DTT forecasted a severe areal reduction and complete separation of three large habitat fragments due to climate change alone.

Population-level models that consider individual dispersal ability as well as spatial metrics of remaining habitat fragments are needed to determine if such fragmentation is likely to restrict gene flow and lead to local extirpations (Schnell et al., 2013a). Risk assessments derived from such quantitative analyses of fragmentation have demonstrated that currently assigned IUCN categories often underestimate the true extinction risks of species (Schnell et al., 2013b). Similar analyses are necessary to determine if climate change-driven increases in habitat fragmentation in conjunction with the projected decrease in range size are severe enough to qualify *G. roberti* for the Near Threatened or Vulnerable category in the near future. Deteriorating habitat, increased fragmentation, and a decrease in the number of occupied locations are all factors that contribute to extinction risk and are considered in IUCN assessments. Although the forested portion of the consensus estimate for 2050 was greater than the AOO for the Vulnerable IUCN category, it comprised less than a quarter of the current range. Moreover, we reiterate that these areal calculations should be interpreted as upper bounds of AOO; they likely overestimate it, for example because they were based on land cover data at a relatively coarse grain and included many small disjunct areas of suitable habitat unlikely to be occupied by the species. Considering the additional unrealistically optimistic assumption of no forest loss after 2010 (the most recent available MODIS layer), the rapid projected range reduction was a disconcerting sign of climate change vulnerability for a species in the LC category.

4.3. Forest cover and conservation actions

Our analysis of forest cover requirements from relatively coarse remotely sensed data was an informative tool for a species with sparse insights into its natural history. With limited information about preferred microhabitat and vegetation, or individual home range size, data on forest cover at a scale somewhat coarse for a small non-volant mammal might nonetheless reveal more about the habitat tolerances than higher-resolution datasets (Sexton et al., 2016). By using two different thresholds, we were able to capture some of the uncertainty regarding its deforestation tolerance. The relatively low minimum forest cover threshold of 18% signified that the species was found in sparsely forested areas, which correspond to higher levels of disturbance and deforestation. This may be indicative of tolerance to habitat modification, which is consistent with some available information on *G. roberti* (Carleton and Goodman, 2003). Exercising caution when inferring disturbance tolerance from few data points, the more conservative 40% DTT identified presumably more "pristine habitat" as recommended for conservation by the latest assessment (Kennerley, 2016). The places considered sufficient by the conservative threshold but not the more permissive one could be targeted for habitat restoration efforts, especially in key corridor areas to improve connectivity among habitat fragments (Rudnick et al., 2012). Additionally, the relatively high tolerance to disturbance suggested by our analyses may signify that *G. roberti* can fare well in mixed-use PAs, where some resource extraction is allowed.

The analysis of habitat protection for *G. roberti* emphasized the need to account for future climate change in current conservation planning. Despite the projected reduction in the extent of suitable habitat, including the potential loss of suitability in several PAs, we found *G. roberti* to be adequately protected by Madagascar's current PA system, with future preservation of the species' habitat dependent on the efficiency of these PAs at halting further deforestation. This presents a formidable challenge, as rapid recent PA system expansion outpaced increases in funding availability, community engagement, and enforcement efficiency (Gardner et al., 2018). Many PAs remain "paper parks" that lack management, while ecosystem degradation is expected to continue in mixed-use PAs if natural resource harvesting exceeds ecologically sustainable levels. However, even highly efficient PA systems have to account for the challenges presented by climate change, and several studies have investigated the adequacy of the IUCN Red List criteria for providing enough warning time for conservation efforts (Thomas et al., 2011; Hannah, 2012; Stanton et al., 2015). Worrisome loss of climatic suitability within existing PA boundaries has supported proposals for dynamic PA systems where underperforming reserves are replaced by new ones to reflect changing conservation priorities (Fuller et al., 2010; Alagador et al., 2014). In this study, we combined two forest cover thresholds with multi-RCP and multi-GCM estimates of climate not only to identify areas of high priority, but also to explicitly address uncertainties associated with forecasting species distributions under climate change. The results provide a better understanding of the environmental challenges that might threaten the existence of poorly known tropical montane mammals, and similar methodologies could be used to estimate the efficiency of conservation planning for other species that are not well characterized.

Although forecasts of trends in habitat suitability and identification of key areas for protection have clear implications for conservation, the promise of studies such as this one for practice-oriented conservation planning has limitations that can be ameliorated by software development and increased capacity building. Besides the well-documented gap between conservation assessments and their implementation (Knight et al., 2006), to date the practical contribution of SDM-based approaches to decision-making processes such as reserve selection is not clear (Cayuela et al., 2009; Guisan et al., 2013). Keeping up with the recent proliferation of cutting-edge methodological advancements in the SDM field (Araújo et al., 2019) requires programming and modeling skills, unfortunately making this tool inaccessible to many conservation practitioners. Effective dissemination of methodological techniques for use by a broader audience is crucial for successful translation of conservation assessments to on-the-ground action. Platforms that provide access to advanced modeling techniques to users of varying backgrounds, from modelers to non-specialists, are necessary to bridge this gap (Kass et al., 2018). Greater accessibility of SDM methodologies to practitioners at different stages of conservation planning also invites multiple perspectives from different fields, hopefully leading to more effective execution of suggested conservation actions. Broader application of this tool and estimates that can be derived from it – like in the worked example here – is critical to the design of conservation practices aimed to minimize the negative effects of land use change and climate change on biodiversity.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

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References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Viela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545.

Alagador, D., Cerdeira, J.O., Araújo, M.B., 2014. Shifting protected areas: scheduling spatial priorities under climate change. J. Appl. Ecol. 51, 703–713.

Anderson, R.P., 2013. A framework for using niche models to estimate impacts of climate change on species distributions. Ann. N. Y. Acad. Sci. 1297, 8–28.

Anderson, R.P., Martínez-Meyer, E., 2004. Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. Biol. Conserv. 116, 167–179.

Anderson, R.P., Raza, A., 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. J. Biogeogr. 37, 1378–1393.

Araújo, M.B., Peterson, A.T., 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93, 1527–1539.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecol. Lett. 14, 484–492.

Araújo, M.B., Anderson, R.P., Márcia Barbosa, A., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E., Rahbek, C., 2019. Standards for distribution models in biodiversity assessments. Sci. Adv. 5, eaat4858.

Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol. Model. 157, 101–118.

Austin, M.P., Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. J. Biogeogr. 38, 1–8.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S., Peterson, A., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 222, 1810–1819.

Beresford, A.E., Buchanan, G.M., Donald, P.F., Butchart, S.H.M., Fishpool, L.D.C., Rondinini, C., 2011. Poor overlap between the distribution of protected areas and globally threatened birds in Africa. Anim. Conserv. 14, 99–107.

Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol. Model. 275, 73–77.

Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2017. A single-algorithm ensemble approach to estimating suitability and uncertainty: cross-time projections for four Malagasy tenrecs. Divers. Distrib. 23, 196–208.

Brooks, T.M., Pimm, S.L., Akçakaya, H.R., Buchanan, G.M., Butchart, S.H.M., Foden, W., Hilton-Taylor, C., Hoffmann, M., Jenkins, C.N., Joppa, L., Li, B.V., Menon, V., Ocampo-Peñuela, N., Rondinini, C., 2019. Measuring terrestrial Area of Habitat (AOH) and its utility for the IUCN Red List. Trends Ecol. Evol. 34, 977–986.

Brown, K.A., Parks, K.E., Bethell, C.A., Johnson, S.E., Mulligan, M., 2015. Predicting plant diversity patterns in Madagascar: understanding the effects of climate and land cover change in a biodiversity hotspot. PLoS One 10, e0122721.

Carleton, M.D., Goodman, S.M., 2003. *Gymnuromys*. In: Goodman, S.M., Benstead, J.P. (Eds.), The Natural History of Madagascar. The University of Chicago Press, Chicago, pp. 1381–1383.

Cayuela, L., Golicher, D.J., Newton, A.C., Kolb, M., de Alburquerque, F.S., Arets, E.J.M.M., Alkemade, J.R.M., Pérez, A.M., 2009. Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. Trop. Conserv. Sci. 2, 319–352.

DiMiceli, C.M., Carroll, M.L., Sohlberg, R.A., Huang, C., Hansen, M.C., Townsend, J.R.G., 2011. Annual Global Automated MODIS Vegetation Continuous Fields (MOD44B), 250 m Spatial Resolution, Collection. University of Maryland, College Park.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.McC.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 4, 330–342.

Foden, W.B., Young, B.E., Akçakaya, H.R., Garcia, R.A., Hoffmann, A.A., Stein, B.A., Thomas, C.D., Wheatley, C.J., Bickford, D., Carr, J.A., Hole, D.G., Martin, T.G., Pacifici, M., Pearce-Higgins, J.W., Platts, P.J., Visconti, P., Watson, J.E.M., Huntley, B., 2019. Climate change vulnerability assessment of species. Wiley Interdiscip. Rev. Clim. Change 10, e551.

Fuller, R.A., McDonald-Madden, E., Wilson, K.A., Carwardine, J., Grantham, H.S., Watson, J.E.M., Klein, C.J., Green, D.C., Possingham, H.P., 2010. Replacing underperforming protected areas achieves better conservation outcomes. Nature 466, 365–367.

Galante, P.J., Alade, B., Muscarella, R., Jansa, S.A., Goodman, S.M., Anderson, R.P., 2018. The challenge of modeling niches and distributions for data-poor species: a comprehensive approach to model complexity. Ecography 41, 726–736.

Gardner, C.J., Nicoll, M.E., Birkinshaw, C., Harris, A., Lewis, R.E., Rakotomalala, D., Ratsifandrihamanana, A.N., 2018. The rapid expansion of Madagascar's protected area system. Biol. Conserv. 220, 29–36.

Gerstner, B.E., Kass, J.M., Kays, R., Helgen, K.M., Anderson, R.P., 2018. Revised distributional estimates for the recently discovered olinguito (*Bassaricyon neblina*), with comments on natural and taxonomic history. J. Mammal. 99, 321–332.

Goberville, E., Beaugrand, G., Hautekeete, N.C., Piquot, Y., Luczak, C., 2015. Uncertainties in the projection of species distributions related to general circulation models. Ecol. Evol. 5, 1100–1116.

Goodman, S.M., Benstead, J.P., 2005. Updated estimates of biotic diversity and endemism for Madagascar. Oryx 39, 73–77.

Goodman, S.M., Soarimalala, V., Raheriarisena, M., Rakotondravony, D., 2013. Small mammals or tenrecs (Tenrecidae) and rodents (Nesomyidae). In: Goodman, S.M., Raherilalao, M.J. (Eds.), Atlas of Selected Land Vertebrates of Madagascar. Association Vahatra, Antananarivo.

Goodman, S.M., Raherilalao, M.J., Wohlhauser, S., 2018. The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota. Association Vahatra, Antananarivo.

Grainger, A., 1999. Constraints on modelling the deforestation and degradation of tropical open woodlands. Glob. Ecol. Biogeogr. 8, 179–190.

Grinand, C., Rakotomalala, F., Gond, V., Vaudry, R., Bernoux, M., Vieilledent, G., 2013. Estimating deforestation in tropical humid and dry forests in Madagascar from 2000 to 2010 using multi-date Landsat satellite images and the random forests classifier. Remote Sens. Environ. 139, 68–80.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435.

Hannah, L., 2012. Saving a Million Species: Extinction Risk from Climate Change. Island Press, Washington, D.C.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. Front. Ecol. Environ. 5, 131–138.

Harper, G.J., Steininger, M.K., Tucker, C.J., Juhn, D., Hawkins, F., 2007. Fifty years of deforestation and forest fragmentation in Madagascar. Environ. Conserv. 34, 325–333.

Harris, G., Pimm, S.L., 2008. Range size and extinction risk in forest birds. Conserv. Biol. 22, 163–171.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hurlbert, A.H., Jetz, W., 2007. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. Proc. Natl. Acad. Sci. 104, 13384–13389.

IPCC, 2013. Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IUCN, 2012. IUCN Red List Categories and Criteria: Version 3.1, Second ed. IUCN, Gland, Switzerland and Cambridge, UK.

IUCN Standards and Petitions Committee, 2019. Guidelines for Using the IUCN Red List Categories and Criteria, Version 14. IUCN Standards and Petitions Subcommittee, ⟨http://www.iucnredlist.org/documents/RedListGuidelines.pdf⟩.

Jansa, S.A., Soarimalala, V., Goodman, S.M., Barker, F.K., 2008. Morphometric variation and phylogeographic structure in *Macrotarsomys bastardi* (Rodentia: Nesomyidae), an endemic Malagasy dry forest rodent. J. Mammal. 89, 316–324.

Jenkins, C.N., Pimm, S.L., Joppa, L.N., 2013. Global patterns of terrestrial vertebrate diversity and conservation. Proc. Natl. Acad. Sci. 110, E2602–E2610.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356, 270–275.

Kass, J.M., Vilela, B., Aiello-Lammens, M.E., Muscarella, R., Merow, C., Anderson, R.P., 2018. Wallace: a flexible platform for reproducible modeling of species niches and distributions built for community expansion. Methods Ecol. Evol. 9, 1151–1156.

Kass, J.M., Meenan, S.I., Tinoco, N., Burneo, S.F., Anderson, R.P., 2021. Improving area of occupancy estimates for parapatric species using distribution models and support vector machines. Ecol. Appl. 31, e02228.

Kennerley R., 2016. *Gymnuromys roberti*. The IUCN Red List of Threatened Species 2016: e.T9581A22237297. Available from ⟨http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T9581A22237297.en⟩ (Accessed March 2019).

Knight, A.T., Driver, A., Cowling, R.M., Maze, K., Desmet, P.G., Lombard, A.T., Rouget, M., Botha, M.A., Boshoff, A.F., Castley, J.G., Goodman, P.S., Mackinnon, K., Pierce, S.M., Sims-Castley, R., Stewart, W.I., Von Hase, A., 2006. Designing systematic conservation assessments that promote effective implementation: best practice from South Africa. Conserv. Biol. 20, 739–750.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S.J., Thomas, C.D., Beentje, H., Dransfield, J., Fisher, B.L., Glaw, F., Good, T.C., Harper, G.J., Hijmans, R.J., Lees, D.C., Louis, E., Nussbaum, R.A., Raxworthy, C.J., Razafimpahanana, A., Schatz, G.E., Vences, M., Vieites, D.R., Wright, P.C., Zjhra, M.L., 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science 320, 222–226.

La Sorte, F.A., Jetz, W., 2010. Projected range contractions of montane biodiversity under global warming. Proc. R. Soc. B 277, 3401–3410.

Li, B.V., Hughes, A.C., Jenkins, C.N., Ocampo-Peñuela, N., Pimm, S.L., 2016. Remotely sensed data informs Red List evaluations and conservation priorities in Southeast Asia. PLoS One 11, e0160566.

McCain, C.M., Colwell, R.K., 2011. Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecol. Lett. 14, 1236–1245.

Merow, C., Smith, M.J., Silander Jr., J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36, 1058–1069.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol. Evol. 5, 1198–1205.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Ocampo-Peñuela, N., Jenkins, C.N., Vijay, V., Li, B.V., Pimm, S.L., 2016. Incorporating explicit geospatial data shows more species at risk of extinction than the current Red List. Sci. Adv. 2, e1601367.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, T.A., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34, 102–117.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. Ecological Niches and Geographic Distributions. Monographs in Population Biology 49 Princeton University Press, Princeton.

Peterson, A.T., Navarro-Sigüenza, A.G., Gordillo, A., 2016. Assumption- versus data-based approaches to summarizing species' ranges. Conserv. Biol. 32, 568–575.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.

Pimm, S.L., Harris, G., Jenkins, C.N., Ocampo-Peñuela, N., Li, B.V., 2017. Unfulfilled promise of data-driven approaches: response to Peterson et al. 2016. Conserv. Biol. 31, 944–947.

Radosavljevic, A., Anderson, R.P., 2014. Making better Maxent models of species distributions: complexity, overfitting, and evaluation. J. Biogeogr. 41, 629–643.

Rodrigues, A.S.L., 2011. Improving coarse species distribution data for conservation planning in biodiversity-rich, data-poor, regions: no easy shortcuts. Anim. Conserv. 14, 108–110.

Rudnick, D.A., et al., 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues Ecol. 16, 1–20.

Schnell, J.K., Harris, G.M., Pimm, S.L., Russel, G.J., 2013a. Quantitative analysis of forest fragmentation in the Atlantic Forest reveals more threatened bird species than the current Red List. PLoS ONE 8, e65357.

Schnell, J.K., Harris, G.M., Pimm, S.L., Russell, G.J., 2013b. Estimating extinction risk with metapopulation models of large-scale fragmentation. Conserv. Biol. 27, 520–530.

Sexton, J.O., Noojipady, P., Song, X.P., Feng, M., Song, D.X., Kim, D.H., Anand, A., Huang, C., Channan, S., Pimm, S.L., Townshend, J.R., 2016. Conservation policy and the measurement of forests. Nat. Clim. Change 6, 192–196.

Shcheglovitova, M., Anderson, R.P., 2013. Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. Ecol. Model. 269, 9–17.

Soarimalala, V., Goodman, S.M., 2011. Les Petits Mammifères de Madagascar. Association Vahatra, Antananarivo.

Stanton, J.C., Shoemaker, K.T., Pearson, R.G., Akçakaya, H.R., 2015. Warning times for species extinctions due to climate change. Glob. Change Biol. 21, 1066–1077.

Styger, E., Rakotondramasy, H.M., Pfeffer, M.J., Fernandes, E.C.M., Bates, D.M., 2007. Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. Agric. Ecosyst. Environ. 119, 257–269.

Thomas, C.D., Hill, J.K., Anderson, B.J., Bailey, S., Beale, C.M., Bradbury, R.B., Bulman, C.R., Crick, H.Q.P., Eigenbrod, F., Griffiths, H.M., Kunin, W.E., Oliver, T.H., Walmsley, C.A., Watts, K., Worsfold, N.T., Yardley, T., 2011. A framework for accessing threats and benefits to species responding to climate change. Methods Ecol. Evol. 2, 125–142.

UNEP-WCMC. Protected Area Profile for Madagascar from the World Database of Protected Areas. Available at: ⟨www.protectedplanet.net⟩. (Accessed February 2019).

Urban, M.C., 2015. Accelerating extinction risk from climate change. Science 348, 571–573.

Vieilledent, G., Grinand, C., Rakotomalala, F.A., Ranaivosoa, R., Rakotoarijaona, J.R., Allnutt, T.F., 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.

Warren, D.L., Wright, A.N., Seifert, S.N., Shaffer, H.B., 2014. Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. Divers. Distrib. 20, 334–343.

Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H., Veran, S., 2013. Presence-only modelling using MAXENT: when can we trust the inferences? Methods Ecol. Evol. 4, 236–243.