

# The fate of Madagascar's rainforest habitat

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**Madagascar has experienced extensive deforestation and overharvesting, and anthropogenic climate change will compound these pressures. Anticipating these threats to endangered species and their ecosystems requires considering both climate change and habitat loss effects. The genus *Varecia* (ruffed lemurs), which is composed of two Critically Endangered forest-obligate species, can serve as a status indicator of the biodiverse eastern rainforest of Madagascar. Here, we combined decades of research to show that the suitable habitat for ruffed lemurs could be reduced by 29–59% from deforestation, 14–75% from climate change (representative concentration pathway 8.5) or 38–93% from both by 2070. If current protected areas avoid further deforestation, climate change will still reduce the suitable habitat by 62% (range: 38–83%). If ongoing deforestation continues, the suitable habitat will decline by 81% (range: 66–93%). Maintaining and enhancing the integrity of protected areas, where rates of forest loss are lower, will be essential for ensuring persistence of the diversity of the rapidly diminishing Malagasy rainforests.**

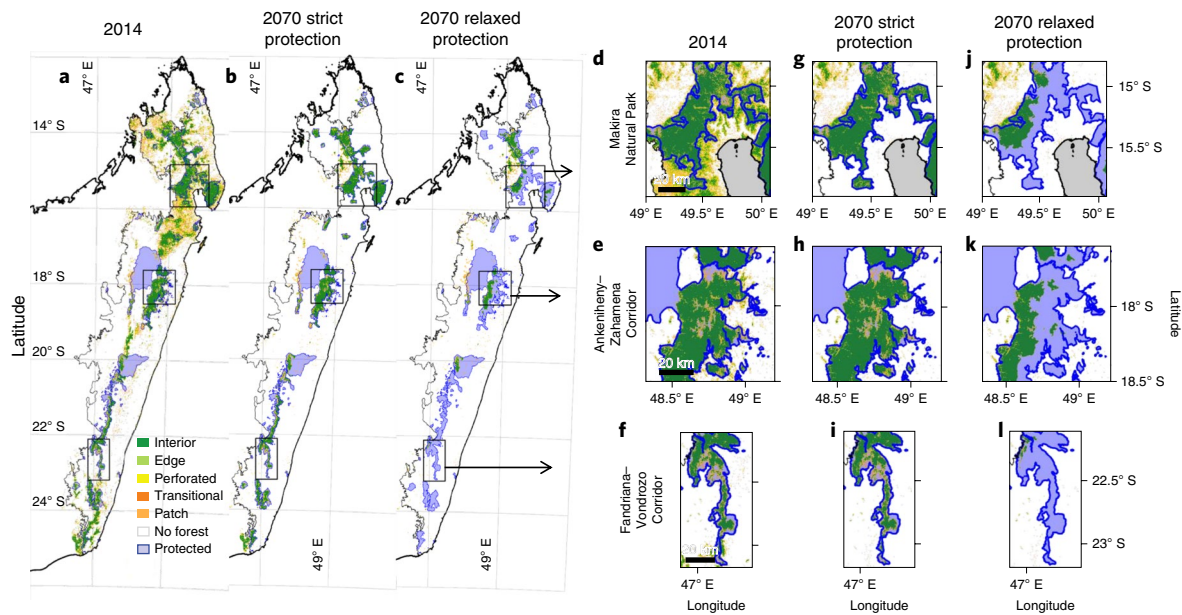
Extinction due to human causes represents the ultimate failure of conservation. Facing concurrent pressures from habitat fragmentation, overharvesting, overhunting, invasive species, pollution and anthropogenic climate change, Earth is entering a sixth mass extinction event<sup>1</sup>. Although conservation biologists recognize a wide range of threats<sup>2,3</sup>, climate change receives special attention owing to its global reach, ability to reshape entire ecosystems and potential to impact areas that are otherwise ‘protected’<sup>4</sup>. Although climate change is becoming one of the greatest threats to Earth’s already-impacted biota<sup>5</sup>, it may not be the most severe threat today and may not become the most severe threat for all species<sup>6</sup>. Indeed, many species are already strongly affected by non-climatic threats such as the degradation and alteration of habitat<sup>3</sup>. Thus, conservation efforts would benefit from investigations into the relative impacts of both climatic and non-climatic threats on vulnerable species<sup>7</sup>.

As one of the world’s ‘hottest’ biodiversity hotspots<sup>8</sup>, Madagascar is experiencing all of the key global change threats, including climate change<sup>9,10</sup>, invasive species<sup>11,12</sup>, overharvesting<sup>13–16</sup> and habitat loss and fragmentation<sup>17–19</sup>. In particular, deforestation reduced

the island’s forest cover by 44% between 1953 and 2014<sup>20</sup>. Climate change is expected to further affect Madagascar’s highly seasonal environments<sup>21,22</sup>. These challenges are particularly dire since Madagascar is home to 5% of the world’s biodiversity, of which approximately 90% is endemic<sup>23–25</sup> and much of which is considered threatened with extinction<sup>8,26</sup>. For example, 96% of Madagascar’s 101 lemur species are listed as threatened (Vulnerable, Endangered or Critically Endangered), making them one of the most imperilled groups of vertebrates globally<sup>26</sup>. In the previous decade, large areas of Madagascar were identified for gazetting<sup>21</sup>. Nevertheless, as a country listed in the bottom 15% on the United Nations (UN) Human Development Index (<http://hdr.undp.org/en/composite/HDI>), resources are limited for species conservation and natural resource management. There are also questions regarding the ability of managers within protected areas to effectively safeguard local species and habitats from hunting and exploitation of forest products<sup>27</sup>.

To guide the use of limited resources most effectively, we determine how climate change and deforestation could affect

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**Fig. 1 | Current and future predicted fragmentation class of the eastern Madagascar rainforest. a**, Forest fragmentation class in 2014 (data from ref. <sup>20</sup>). **b**, Forest fragmentation in 2070 assuming no new deforestation in protected areas. **c**, Forest fragmentation in 2070 assuming deforestation can occur anywhere. The black outline within Madagascar encompasses the eastern rainforest ecoregion<sup>20</sup>. **d–l**, Focal regions highlighted in Figs. 3–5 for 2014 (**d–f**) and 2070 under strict (**g–i**) and relaxed (**j–l**) protection: Makira Natural Park (**d,g,j**), Ankeniheny–Zahamena Corridor (CAZ; **e,h,k**) and the southern end of the Fandriana–Vondrozo Corridor (COFAV; **f,i,l**). The grey area in the Makira panels represents Antongil Bay.

Madagascar's rainforest habitat over the next several decades. We first model rainforest cover change in Madagascar using historical data<sup>20</sup> and projected cover to 2070 assuming either 'strict' protection, in which no new deforestation occurs in protected areas, or 'relaxed' protection, in which protected areas can become deforested. Second, we model the climatic and habitat-based niches of two of Madagascar's Critically Endangered rainforest-dwelling taxa: *Varecia variegata* and *V. rubra*. These two species, collectively composing the ruffed lemur genus, are indicators and determinants of rainforest health in Madagascar as they are highly sensitive to habitat degradation<sup>28–32</sup>, like much of Madagascar's eastern rainforest fauna<sup>33–36</sup>, and are uniquely responsible for dispersing the seeds of a number of plant species in Malagasy rainforests<sup>37–44</sup>. Thus, the ecological niche of ruffed lemurs is an ideal proxy for healthy rainforest habitat.

Third, we identify future suitable habitats for ruffed lemurs (that is, healthy rainforest habitat) on the basis of the modelled deforestation scenarios in Madagascar and future climatic conditions under representative concentration pathways (RCPs) 2.6, 4.5, 6.0 and 8.5 emissions scenarios<sup>45</sup>. Niche models were projected to 2070 assuming both climate and deforestation proceed. To discern the relative effect of anticipated climate change versus deforestation, we made niche model projections assuming either climate change or deforestation proceeds as predicted while the other is held at present-day values<sup>46</sup>. Ultimately, identifying how rainforest habitat will change over time—whether as a result of climatic or non-climatic variables or both—can serve as an early warning for the persistence of Madagascar's rainforest fauna. Moreover, because habitat change is expected to have a direct impact on ruffed lemur presence, loss of either species will probably have cascading effects on the structure and integrity of the remaining forest<sup>47,48</sup>.

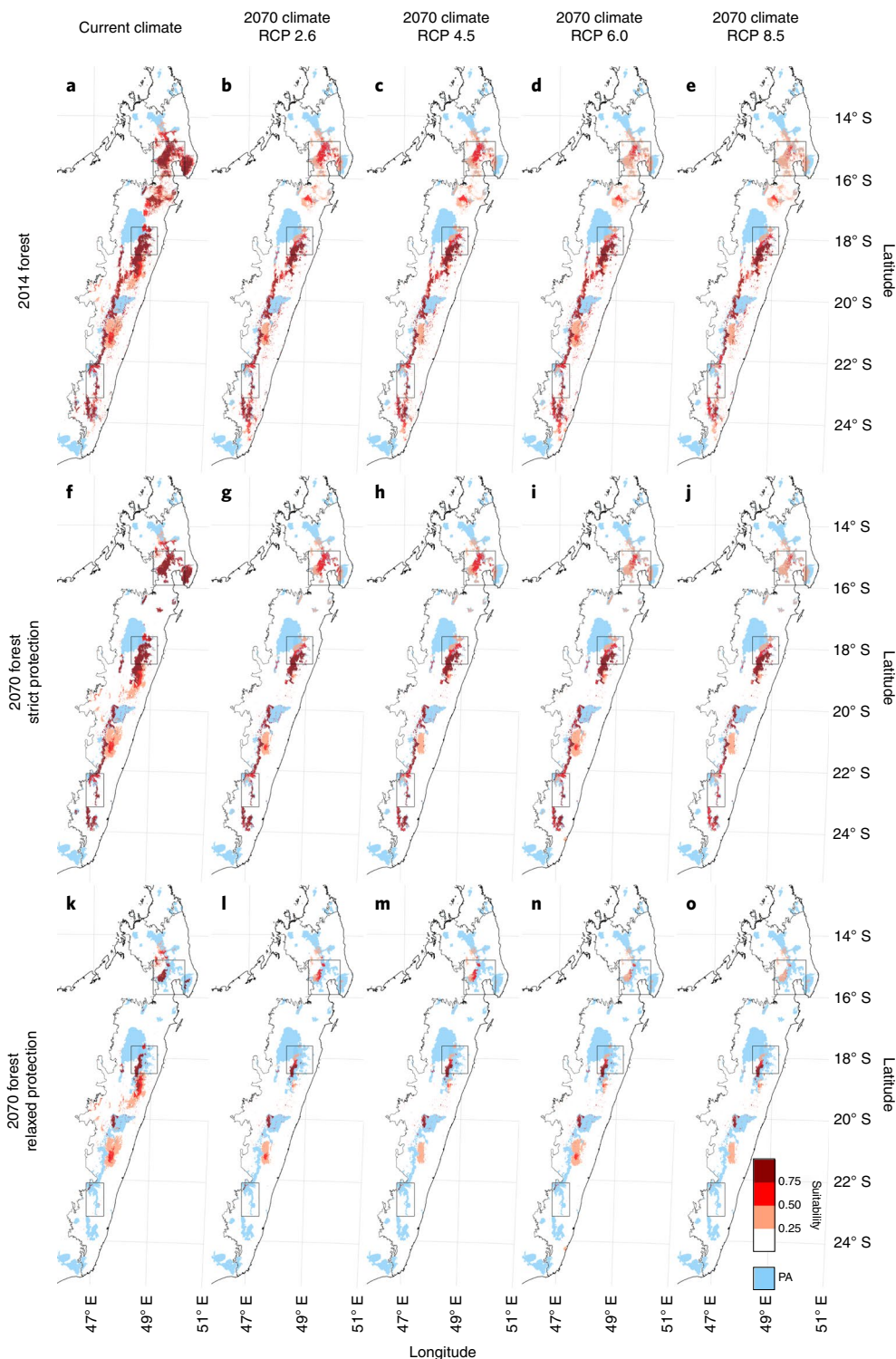
### Projected forest loss in Madagascar

In 2014, there were 45,680 km<sup>2</sup> of forest cover in Madagascar's eastern rainforest<sup>20</sup>. Our projected estimates for rainforest cover change over the next several decades show dramatic declines. When we

consider overall amount of forest loss under a 'relaxed' protection scenario in which deforestation can occur outside and inside protected areas, we estimate that, compared with cover in 2014, 57% of Madagascar's eastern rainforest will remain by 2050 and only 16% by 2070 (Fig. 1, Supplementary Table 1 and Supplementary Methods). Assuming future rates follow the minimum observed rate of deforestation between 2000 and 2014, the entire eastern rainforest is predicted to be lost before 2080. Under a 'strict' protection scenario in which deforestation can only occur outside protected areas, losses are curtailed: forest cover declines to 65% by 2050 and to 51% by 2070. Currently, 30,220 km<sup>2</sup> of forest classifies as 'interior', representing 66% of existing forest cover. Under relaxed protection, interior forest increases to 77% of total cover in 2050 as deforestation removes fragmented and transitional wooded areas, then declines to 46% in 2070 as continued deforestation increases the amount of non-interior habitat. Under strict protection, interior forest increases to 83% of total cover by 2050 but then declines to 75% by 2070. Remaining forest tends to be concentrated in protected areas in both scenarios since deforestation is currently lower in protected areas than in unprotected locations (Supplementary Table 2 and ref. <sup>49</sup>).

### Global change and Madagascar's eastern rainforest habitat

Of the remaining eastern rainforest, suitable habitat for *Varecia* will decline moderately or severely, depending on the scenario (Fig. 2 and Supplementary Table 4). By 2070, deforestation alone (with no climate change) is expected to reduce mean habitat suitability by 29% under the strict protection scenario and 59% under the relaxed protection scenario. Climate change alone (with no deforestation) under RCP 8.5 is projected to have an impact similar in magnitude to a relaxed deforestation scenario (with no climate change), with declines in suitable habitat of 46% (mean across five global climate models; range: 14–75%). Combined, climate change and deforestation will dramatically reduce suitable habitat, with mean declines of 62% (range: 38–83%) under strict protection to 81% (66–93%) under relaxed protection.

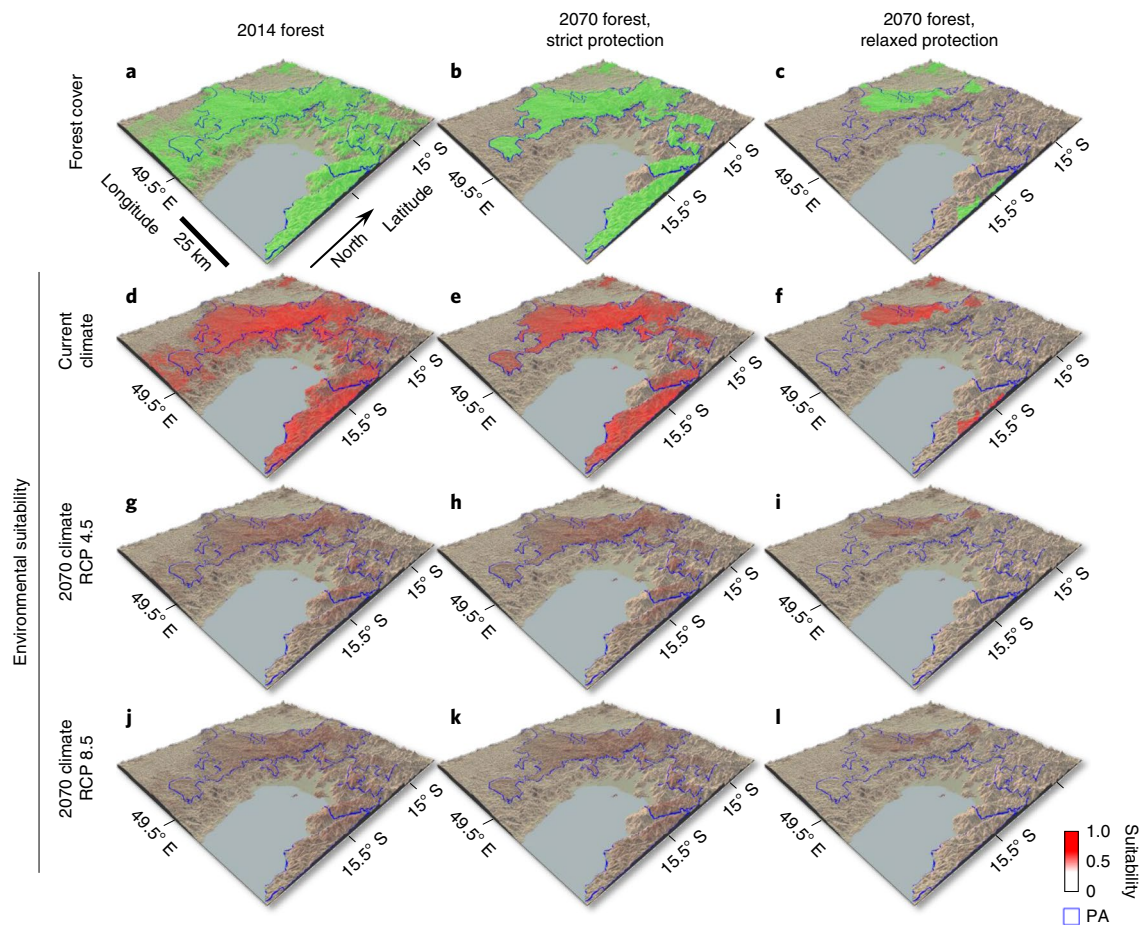


**Fig. 2 | Environmental suitability for ruffed lemurs for the present and the 2070s.** **a**, Suitability given current climate and forest cover. **f,k** How deforestation under strict (**f**) and relaxed (**k**) forest protection affects suitability while climate is held at its current state. **b–e**, The effect of climate change by the 2070s under RCP scenarios 2.6 (**b**), 4.5 (**c**), 6.0 (**d**) and 8.5 (**e**), respectively, while holding forest at its current cover. **g–j–o**, Combinations of deforestation and climate change. The three rectangles denote the Makira Natural Park area (northernmost), the CAZ (middle) and the COFAV (southernmost) detailed in Figs. 3–5. Blue shading represents protected area (PA). For climate change scenarios, results are the projection across the average of five Earth system model projections for 2061–2080.

Region-wide declines belie heterogeneity in impacts of climate change, deforestation and their combined effects. For example, in Makira Natural Park in northeastern Madagascar, climate change reduces habitat suitability severely even if forest cover is held at 2014

levels (Fig. 3a,d,g,j). In other regions, climate change and deforestation interact to reduce the suitability of areas that remain uninhabitable. For example, in the Ankeniheny–Zahamena Corridor in central Madagascar, deforestation alone reduces the extent of





**Fig. 3 | Deforestation and the combined effects of deforestation and climate change on ruffed lemur habitat suitability for the Makira focal area.** **a–l**, Maps show scenarios for deforestation (**a–c**) and environmental suitability for ruffed lemurs (**d–l**) in the current period (**a,d,g,j**) and the 2070s (**b,c,e,f,h,i,k,l**). Climate changes reduce suitability dramatically even if no further deforestation occurs (**d,g,j**). Blue outlines encompass protected areas (PA). For climate change scenarios, images represent the average projection across five Earth system models. To aid visual interpretation, elevation is exaggerated by a factor of four relative to horizontal distance. Forest cover in **a** is from ref. <sup>20</sup>.

highly suitable area (Fig. 4d–f) whereas, acting alone, climate change restricts suitable area to the southern part of the region (Fig. 4a,d,g,j). Finally, deforestation has the potential to decimate *Varecia* populations even if climate change has less effect, such as in the Fandriana–Vondrozo Corridor in the south (Fig. 5d–f). In this case, climate change and deforestation combined almost entirely eliminate suitable habitat (Fig. 5l).

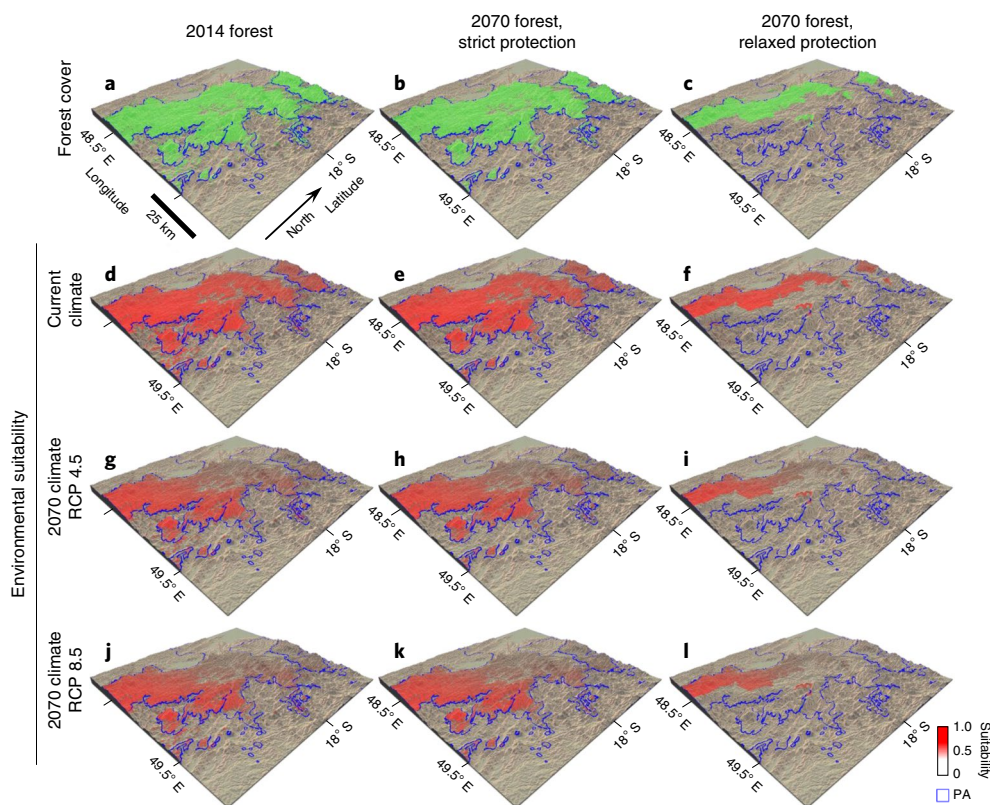
### Interacting effects of global change

The effects that climate change has on biodiversity will interact with ongoing and growing threats from other drivers of global change in eastern Madagascar, including invasive species<sup>50</sup> and overexploitation<sup>51</sup>. Indeed, these drivers may be as important or even more important in defining the conservation trends of vulnerable species<sup>6,52</sup>. Projecting distributions just several decades into the future, we found that forest loss and climate change, as well as their interaction, severely reduce suitable habitat for ruffed lemurs. Of these, deforestation appears to be the more pressing threat, as even under a hypothetical scenario with ‘optimistic’ rates of forest loss, the eastern rainforest effectively suffers complete loss before 2080. In fact, suitable habitat cover is projected to be reduced on average to less than half of current cover within the next 50 years, even under the strict protection of existing protected areas (Supplementary Tables 1 and 6). We anticipate that this will mean as much as a 38–93%

decline in remaining ruffed lemur numbers by 2070, with cascading effects for the structure and integrity of the forests they inhabit (Supplementary Table 4)<sup>47,48</sup>. Our results demonstrate that, despite the dramatic risks associated with anthropogenic climate change, effects from other global changes must remain in focus; we highlight deforestation here, but consideration should also be given to invasive species, hunting and wildlife trafficking.

While our analysis predicts a daunting reduction of primary eastern rainforest, it also may be ‘optimistic’ given our assumptions about the drivers and pace of forest loss and climate change<sup>7</sup>. For example, to allow any forest to remain by 2070, we had to assume deforestation rates followed the minimum rate across 2000–2014. Nonetheless, the rate of forest loss since the 1950s has been highly variable<sup>20</sup>, which suggests that assuming a constant loss rate is unrealistic. Moreover, for the island as a whole, the most recent deforestation rate is among the highest recorded since 1953<sup>20</sup>, and for the eastern rainforest in particular, the most recent rate was the highest across the three periods used here.

Likewise, our study ignores climate-induced changes in forest cover and composition. It is possible that climate change could alter forest structure and composition to open high-elevation forests currently avoided by *Varecia*, if suitable dispersal corridors exist. However, the amount of habitat in these areas is dwarfed by the projected losses at lower elevations (Supplementary Table 5). Without dramatic socioeconomic and policy change, current



**Fig. 4 | Deforestation and the combined effects of deforestation and climate change on ruffed lemur habitat suitability for the CAZ focal area. a–l.** Maps show scenarios for deforestation (a–c) and environmental suitability for ruffed lemurs (d–l) in the current period (a,d,g,j) and the 2070s (b,c,e,f,h,i,k,l). Climate change and deforestation act together (h,i,k,l) to reduce habitat suitability more than climate change (g,i) or deforestation (e,f) acting alone. See caption for Fig. 3 for further explanation. Forest cover in a is from fig. 20.

emissions (including commitments to cut emissions) could send climate on a ‘high’ change trajectory akin to RCP 8.5<sup>45</sup>. Even if emissions are drastically and quickly curtailed, a scenario similar to RCP 2.6 still greatly diminishes habitat quality in the eastern rainforest of Madagascar due to deforestation (Fig. 2g,l).

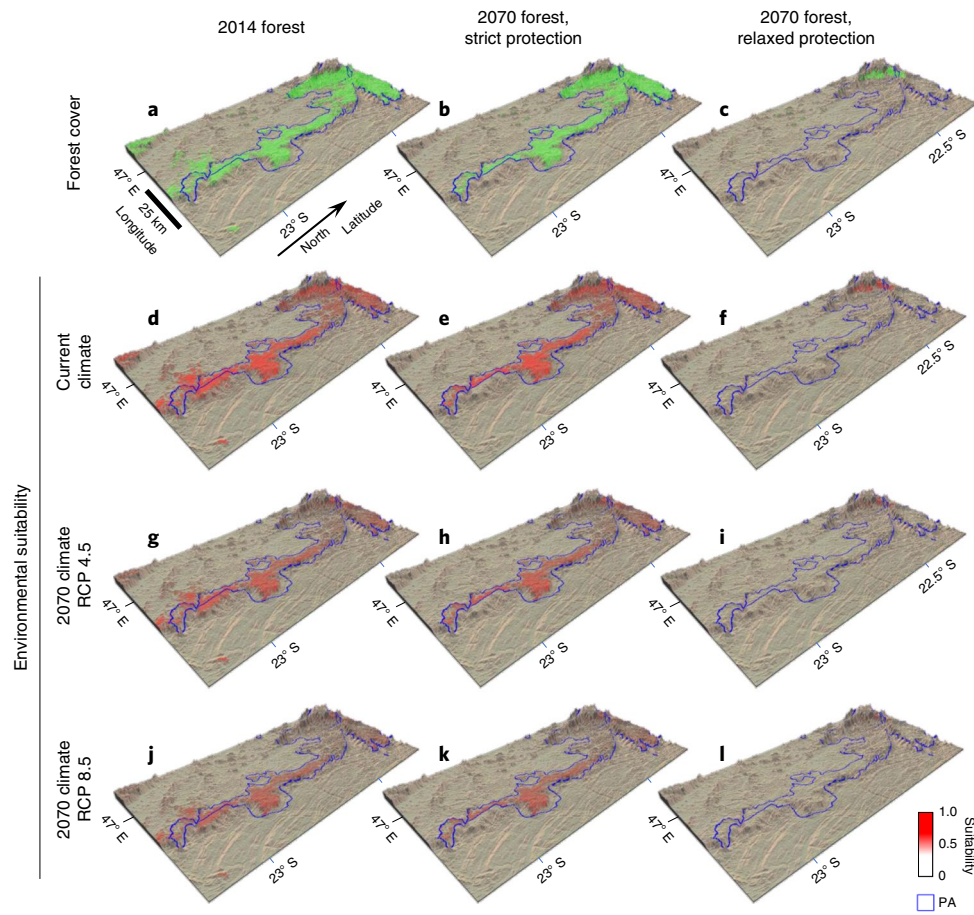
Importantly, our model assumes that the incentives driving deforestation do not respond to climate change, but we do not expect this to be the case. Climate change could alter local people’s ability to produce and access agricultural and wild foods, disproportionately affecting smallholder farmers<sup>53</sup>. With reduced agricultural productivity<sup>53</sup> and threats to accessing seafood<sup>54</sup>, the rapidly growing Malagasy population may be forced to further encroach on protected forest areas to produce food. Because 85% of the Malagasy population resides in rural areas, this scenario poses a substantial threat to food production and food security. In a global analysis, Madagascar was ranked first as the country most likely to have future civil conflicts arise from tensions between food security and biodiversity conservation<sup>55</sup>, as perhaps foreshadowed by recent violence against park managers and communities<sup>56</sup>.

The effects of climate change on human behaviour will likely increase not only indirect threats to ruffed lemurs through habitat loss but also direct threats through increased hunting. Ruffed lemurs are hunted across Madagascar at a rate of 1 to 7 animals per 100 households per year<sup>16,57</sup>. Among lemurs, they are preferred for their taste and are caught throughout their range in the Makira watershed<sup>16,58</sup>, on the Masoala Peninsula<sup>29,59</sup>, in the Alaotra-Mangoro region<sup>27</sup> and in Kianjavato<sup>57</sup>. Further, hunters often specifically target intact forests in rural regions where ruffed lemur densities are highest<sup>60</sup>. In these remote regions, poor and food-insecure households hunt more wildlife than do those that are food secure<sup>15,54</sup>.

Food-insecure hunters may not only clear additional ruffed lemur habitat for their crops but also have more incentive to travel farther to remaining habitats to hunt these animals for food. Thus, even supposedly protected areas identified by our analysis may not be immune to other pressing threats.

Past deforestation (especially in warmer, lowland areas; T. Steffens and S.M.L., manuscript in preparation) and hunting, which are often related<sup>61</sup>, may have reduced the range of ruffed lemurs such that it is truncated relative to the climate conditions the lemurs can tolerate<sup>62,63</sup>. If so, then the climate component of the niche model may underestimate climatic tolerances. Indeed, occurrences of ruffed lemurs extend to the lowest, warmest elevations (1.0% of all occurrences from 0 to 100 m elevation, 1.2% between 100 and 200 m and 1.0% from 200 to 300 m), whereas forest cover classified as ‘interior’ occurs at about three times that rate in the same elevation bands (in 2014, 3.3% of cover from 0 to 100 m, 3.0% from 100 to 200 m and 2.5% from 200 to 300 m), which is suggestive of population thinning in lowland regions. However, we addressed this potential complication by using a weighting scheme to correct for sparse records in areas that may have missing lemur populations due to non-climatic factors (Supplementary Fig. 3). In addition, our models used only sites where ruffed lemurs have been detected (versus also using survey sites without detections, which might be indicative of hunting and other factors not reflected by the predictors in the model). Finally, we combined data from the two congeneric species instead of analysing the species separately. This method, justified by extensive niche overlap and increased realism in responses (Supplementary Figs. 4–6)<sup>62,64,65</sup>, provides a more complete picture of the climatic niche and could advise other studies with similar data constraints.





**Fig. 5 | Deforestation and the combined effects of deforestation and climate change on ruffed lemur habitat suitability for the COFAV focal area. a–l,** Maps show scenarios for deforestation (a–c) and environmental suitability for ruffed lemurs (d–l) in the current period (a,d,g,j) and the 2070s (b,c,e,f,h,i,k,l). Deforestation reduces habitat suitability dramatically even if climate does not change (e,f). See caption for Fig. 3 for further explanation. Forest cover in a is from ref. <sup>20</sup>.

### ‘Cooling’ of a biodiversity hotspot

Our results indicate potential conservation opportunities for ruffed lemurs and any of the rainforest dwellers that rely on forest cover and connectivity: protected areas are vital to species persistence<sup>63</sup>. In the short to medium term, forest protection may be more effective than climate mitigation for conserving rainforest lemurs. Ruffed lemurs have long been considered an indicator species, given their reliance on the fruit of slow-growing, long-lived hardwood trees<sup>28</sup> (N. Beeby and A.L.B., manuscript in preparation), and are among the first lemur species to disappear with selective logging<sup>30</sup>. Concentrating conservation efforts on maintaining the integrity of remaining intact forests by increasing the enforcement of protected areas, addressing the reasons people alter forest habitat in protected areas and promoting the protection and regeneration of additional habitats will buy time to find solutions to the exacerbating effects of global climate change—and of course, reducing deforestation is a primary strategy for mitigating climate change. Ensuring forest cover remains intact in existing protected areas, particularly in corridors that link remaining ruffed lemur strongholds, will greatly reduce loss of suitable habitat and maintain connectivity (gene flow) among remaining populations, although some regions will still inevitably suffer deleterious effects of climate change. Moreover, targeting lemurs as Madagascar’s flagship species, ruffed lemurs among them, for conservation action can help preserve other taxa as well. For example, the loss of ruffed lemurs, and other large-bodied lemur species, could decrease the

recruitment of large-seeded plant species with large biomass<sup>43</sup>, which might also negatively impact other animal taxa that rely on such trees for their survival. More broadly, protecting the forests within the range of ruffed lemurs would mean safeguarding much of Madagascar’s unparalleled endemic biodiversity. For example, eastern rainforests contain the highest levels of both species richness and local endemism for reptiles and amphibians<sup>66</sup>, taxa that are remarkable for their overall endemism (92% and 99%, respectively<sup>67</sup>). Unsurprisingly, eastern rainforests also house a disproportionate amount of Madagascar’s plant diversity, which, parallel to our findings, has been predicted to decline substantially from both deforestation and climate change<sup>7</sup>.

Native terrestrial vertebrate population sizes and geographic distributions have been in an accelerating decline despite evidence of rapid evolutionary change in some species<sup>68</sup>. While land-use change has been identified as the primary negative impact on biodiversity, climate change is increasingly exacerbating the effects of other drivers on terrestrial, as well as marine and freshwater ecosystems on a global scale<sup>68</sup>. Immediate curtailing of human-induced climate change would be necessary to prevent cascading losses of ecosystem services and function<sup>69</sup> and large increases in global extinction risk and biodiversity loss<sup>68</sup> by the end of the century. Given that both floristic and non-primate mammalian diversity can be predicted by lemur biodiversity in Madagascar<sup>70</sup>, the patterns we see in ruffed lemurs will probably be reflected in other rainforest species, as well.

To this end, our study points to areas of relatively intact forest that could be prioritized for protection<sup>71</sup>. Where these areas coincide with climate change refugia (areas relatively buffered from climate change that thus enable species persistence<sup>72</sup>), prioritization will increase protection and even enhance translocation efforts. More generally, we challenge the conservation community to contemplate what should be done if nearly all of Madagascar's rainforest habitat were to be lost. To date, most conservation on the island has focused on establishment of protected areas<sup>73</sup>, but even these are being eroded, albeit at a slower rate. If protected areas are not able to serve their intended purpose, how can we ensure the perpetuation of the richness of Madagascar's biodiversity?

### Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-019-0647-x>.

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## Methods

**Projected forest loss in Madagascar.** We constructed a model of forest cover change using historical data from Vieilledent et al.<sup>20</sup>. The full set of methods is described in the Supplementary Information and summarized here. We defined our study region as the entire extent of the eastern rainforest (to which ruffed lemurs are confined) using a mask for this ecoregion from Vieilledent et al.<sup>20</sup> plus an additional 17.5 km buffer to account for the 12 ruffed lemur survey sites (of 12,389) that fell outside this mask (Supplementary Fig. 2; see methods for ecological niche modelling in the following). We modelled forest cover change within this region at 30 m spatial resolution.

We projected forest cover change using two submodels, one for the overall amount of forest loss (forest recovery is negligible in Madagascar<sup>20</sup>) and one identifying the most likely location of deforestation in each year. In the first submodel, we assumed that the amount of forest loss (the sum of area of pixels with forest cover that transition to 'no forest') was a function of the human demand for forest products and land. Thus, we modelled deforestation amount as a function of total population based on a constant per capita demand for forest estimated from change in forest cover across three periods (2000–2005, 2005–2010 and 2010–2014; maps of forest cover in the years 2000, 2005, 2010 and 2014 from ref.<sup>20</sup> were used to provide start and end values for the periods 2000–2005, 2005–2010 and 2010–2014). We then projected demand to 2080 using the 'standard' projections for Madagascar of United Nations population growth rate<sup>74,75</sup>. We note that forest loss may arise from direct clearing (including purposeful fire) and from inadvertent fires. Unfortunately, we are not able to differentiate between the two causes of forest loss. The annual per capita amount of forest loss for eastern rainforest during the three periods 2000–2005, 2005–2010 and 2010–2014 was 15.39, 14.38 and 25.22 m<sup>2</sup>, respectively. If we set initial forest cover equal to the 2014 level (45,681 km<sup>2</sup>) and assume that future loss trends follow the minimum rate (from 2005 to 2010), the entire eastern rainforest is predicted to be lost by 2077. Assuming future loss follows the mean or maximum rates leads to complete loss by 2074 and 2058, respectively. Since there was little difference between the mean and minimum rate in the year in which complete loss occurred, we elected to use an 'optimistic' scenario in which continued forest loss followed the minimum (least loss) trend.

In the second deforestation submodel, we constructed a model of the location of pixels most likely to be deforested using a Bayesian variable-period logistic model<sup>49</sup>. The initial model included spatial predictors representing longitude, latitude, elevation, topographic slope, protected/unprotected area (binary), distance to nearest settlement, distance to nearest road, distance to coast, distance to nearest major inland water body (rivers and lakes), distance to most recent deforestation, distance to forest edge and forest fragmentation class (calculated using a 5 × 5 cell moving window<sup>49,76</sup>). For a given focal cell, fragmentation class was defined on the basis of two measures of forest cover, proportion of cells occupied by forest in a 5 × 5 cell window (density) and the conditional probability that an immediate neighbour has forest cover given the adjacent cell has cover (connectivity) in the window. Fragmentation class was defined as 'no forest' (density = 0), 'patch' (density < 0.4), 'transitional' (density ≥ 0.4 and < 0.6), 'perforated' (density ≥ 0.6 and connectivity < density), 'edge' (density ≥ 0.6 and connectivity > density) or 'interior' (density = 1)<sup>76</sup>. We conducted model selection following Vieilledent et al.<sup>49</sup>. The final model used longitude, elevation, slope, protected area status, distance to nearest most recent deforestation event and distance to nearest forest edge (Supplementary Table 2). To project deforestation to the future, we first calculated the amount of forest lost then removed forested pixels from the previous year's forest cover map on the basis of the most likely locations of forest loss (Supplementary Fig. 1). Forest cover was projected year by year using the previous year's cover as the 'base' layer for calculating forest fragmentation class, distance to nearest deforestation and distance to nearest forest edge in the current year.

We explored two forest cover change scenarios for each submodel. The first assumed relaxed forest protection, in which forest loss could occur anywhere (in protected areas if the model identified these locations as likely). The second assumed strict protection, in which no further forest loss occurred in current protected areas. To enact this scenario, we simulated forest loss into the future as per the relaxed scenario then masked forest cover in protected areas using 2014 cover. The strict protection scenario thus assumes no new forest loss occurs in protected areas as outside areas are deforested and thus a reduced level of deforestation. It thus also assumes products that would have been obtained from protected areas are foregone.

**The current *Varecia* ecological niche.** The genus *Varecia* is composed of two species: the red ruffed lemurs (*Varecia rubra*) and the black-and-white ruffed lemurs (*Varecia variegata*). The two taxa differ in pelage colouration but are both medium-sized (2–5 kg (ref.<sup>77</sup>)) arboreal quadrupeds that are highly frugivorous (>70% of feeding time devoted to fruit<sup>78</sup>; N. Beeby and A.L.B., manuscript in preparation). Although historically the two species' ranges might have overlapped, their current distributions appear separated by the Antainambalana River<sup>79</sup>. *V. rubra* has a relatively restricted range and is confined largely to the Masoala Peninsula, while *V. variegata* is patchily distributed along Madagascar's eastern rainforests from the Antainambalana River south to the Mananara River; both species generally prefer primary rainforest at low to mid-altitudes (<1,200 m; Fig. 1)<sup>80,81</sup>. Field studies demonstrate that forest cover is a strong determinant of the presence of *V. variegata*<sup>31,82</sup> (Supplementary Fig. 4).

Landscape-scale ruffed lemur presence was derived from detection data ( $N = 1,994$  geographically unique sites) obtained from population sampling conducted between 1990 and 2017 by 15 research teams (Supplementary Table 3). Population sampling included two widely used distance sampling techniques, line transect surveys<sup>83,84</sup>, rapid assessment surveys<sup>85</sup>, capture–mark–resighting<sup>86,87</sup> and targeted behavioural observations<sup>88</sup>.

Records of detection/nondetection were obtained from field expeditions conducted by the authors between 1989 and 2017 (Supplementary Table 3). Altogether we tallied 5,882 occurrences of *V. variegata* and 95 of *V. rubra* (Supplementary Fig. 2). We modelled the niche of each species separately and of the genus with both species combined. Detailed methods are described in Supplementary Methods and Results so are only briefly outlined here. We performed several rounds of preliminary modelling to understand which predictors were most important in delimiting the range of ruffed lemurs, including comparisons among climate data sources (WorldClim Version 2.0 versus CHELSA Version 1.2<sup>82,89</sup>), climatic predictors (temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, mean annual precipitation, precipitation seasonality, precipitation of the wettest quarter and precipitation of the driest quarter), predictors related to land cover, human disturbance and access, and topography (elevation, forest cover, forest loss, distance to forest cover loss, distance to nearest major road, distance to nearest major inland water body and presence of rainforest biome), assuming either a narrow accessible area equal to just the eastern rainforest or a broad accessible area equal to all of Madagascar for selection of background sites<sup>90</sup>, and number of background sites (10,000 versus 100,000<sup>91</sup>). On the basis of these tests, we chose a broad background characterized by 10,000 background sites with a limited set of predictors, including four climate predictors from WorldClim (mean temperature of the warmest quarter, temperature seasonality, precipitation of the wettest quarter and precipitation seasonality<sup>92</sup>) and forest cover fragmentation class. We resampled the climate layers to the 30 × 30 m resolution of the forest data using 'nearest neighbour' interpolation, which does not change the values of the climate layers but simply 'overlays' them onto the finer-scale grid. Thus, the ecological niche models were trained using data at the original resolution of the raw data (30 arcsec for climate and 30 m for forest cover). Bias in survey records arising from spatially aggregated searches was corrected using 1 minus the smoothed density of occupied sites<sup>92</sup> (Supplementary Fig. 3). We used two modelling algorithms, generalized linear models (GLMs) and natural splines (NSs), both of which extrapolate in an easily interpretable manner. For model assessment, we divided the range of each taxon (the two species and the genus) into three mutually exclusive geographic areas<sup>93</sup> while ensuring that each cross-validation fold had at least 15 occupied sites. Model performance was evaluated using a weighted continuous Boyce index (CBI), which represents the correlation between model output and the probability of presence<sup>94,95</sup>. We also trained an 'all-sites' model using all occupied sites for each taxon. From the best set of cross-validated models, we used the associated all-sites model to project vulnerability to climate and habitat change into the future.

GLMs for *Varecia variegata* had good calibration accuracy when assessed against spatially independent data (CBI:  $0.74 \pm 0.20$  (mean  $\pm$  s.d.)) while GLMs for *V. rubra* had comparatively poor and highly variable performance ( $-0.30 \pm 0.59$ ). GLMs for the genus had good calibration accuracy and low variability across cross-validation folds (CBI:  $0.76 \pm 0.08$ ; Supplementary Table 4). For each taxon, the NS models had lower performance and higher variation across cross-validation folds. Because of the poor and variable performance of the NS models, we elected to use results from the GLM ecological niche models.

### Future forest cover and climate change scenarios in the *Varecia* ecological niche.

We used future climate layers for the periods 2041 to 2060 and 2061 to 2080 (hereafter '2050s' and '2070s') for the RCP 2.6, 4.5, 6.0 and 8.5 emissions scenarios obtained from WorldClim Version 1.4<sup>96</sup>. Across the suite of ten Earth system models with projections for each period (including an ensemble projection) available for these scenarios, we chose five that predicted the greatest difference in the selected climate predictors between the present and 2061–2080 under the RCP 8.5 emissions scenario across 30 arcsec cells known to be occupied by the genus. We used the predicted forest fragmentation class layer from the years 2050 and 2070 for the two 'future' fragmentation class layers assuming either the strict or relaxed forest protection scenario. We projected habitat suitability into the future using layers from the five Earth system models. We explored the effects of deforestation and climate change alone and in combination by making predictions to future scenarios assuming (1) no climate change (using present climate) but with deforestation (with strict or relaxed protection), (2) no deforestation (using the 2014 forest cover layer) but with climate change and (3) with both deforestation and climate change.

**Niche overlap.** We assessed overlap in the climatic niche of the two species using null model randomization tests<sup>97,98</sup> based on the four climatic variables used in the niche modelling. Niche overlap was computed by comparing the occupancy of environmental space standardized by the frequency of available environmental space across species<sup>98</sup>. Observed overlap was compared with a distribution of overlap values generated using a null model that randomizes the point locations across the study region. To generate the null models, we employed a flexible procedure based on the 'rotate–translate–reflect' method<sup>99</sup> to control for intra- and

interspecific patterns in range geometry<sup>100</sup>. We used the combined set of all randomized ranges across all iterations to represent the background ('available') environment and computed niche overlap using Warren's *D* and the Spearman rank-correlation coefficient (D. Warren, personal communication).

**Reproducibility.** We conducted all analyses using code primarily based on the *dismo*<sup>101</sup>, *raster*<sup>102</sup>, *geosphere*<sup>103</sup> and *rgeos*<sup>104</sup> packages for the R Statistical Environment version 3.4.4<sup>105</sup>. The deforestation model also used the *phcFM*<sup>49</sup> and *fasterRaster*<sup>106</sup> packages, the latter of which was linked to GRASS GIS 7.4.1<sup>107</sup>. Niche model construction and niche overlap procedures were conducted using the *enmSdm* package<sup>100</sup>. All code is available at <https://github.com/adamlilith/varecia>.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

### Data availability

The data that support the findings of this study are available from the corresponding author on request. Historical forest cover data were obtained from ref. <sup>20</sup>. Climate coverages were obtained from ref. <sup>82</sup>.

### Code availability

All code required to reproduce the results is available at <https://github.com/adamlilith/varecia>.

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### Author contributions

T.L.M. conceived the idea, designed and developed the project, acquired, analysed and interpreted data and wrote the paper. A.B.S. adapted the deforestation model, constructed the niche model and wrote the paper. A.N.M., E.A.B., C.B., R.D., S.F., Z.F., C.D.G., S.M.H., M.I., R.L.J., S.J., T.K., S.M.L., E.E.L.Jr, A.M., H.N.T.R., H.L.L.R., J.R. and O.H.R. designed and developed the project, acquired and interpreted data and contributed to the manuscript text. A.L.B. conceived the idea, designed and developed the project, acquired and interpreted data and wrote the paper.

### Competing interests

The authors declare no competing interests.

### Additional information

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41558-019-0647-x>.

**Correspondence and requests for materials** should be addressed to A.L.B.

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### Software and code

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Data collection All analyses were conducted using R 3.4.4 and GRASS GIS 7.4.1. All code is located at the online repository <https://github.com/adamlilith/varecia>.

Data analysis All analyses were conducted using code based on the *dismo* (Hijmans et al. 2017), *raster* (Hijmans 2017a), *geosphere* (Hijmans 2017b), and *rgeos* (Bivand & Rundel 2018) packages for the R Statistical Environment ver. 3.4.4 (R Core team 2018). The deforestation model also used the *phcfM* (Viellendent 2013) and *fasterRaster* (Smith 2018) packages. The latter was linked to GRASS GIS 7.4.1 (Neteler et al. 2012). Ecological niche model construction and evaluation procedures were conducted using the *enmSdm* package (Smith 2018).

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The data that support the findings of this study are available from the corresponding author upon request. Historical forest cover data were obtained from Vieilledent et al. 2018 Biological Conservation. Climate coverages were obtained from Fick et al. 2017 Int. J. Climatol 37.



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## Ecological, evolutionary & environmental sciences study design

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Study description	In our study we combine three decades of research across Madagascar to analyse the threats to the eastern tropical rainforest using as a case study the two lemurs in the genus <i>Varecia</i> , both of which are Critically Endangered. Specifically, we integrate a newly developed spatially-explicit deforestation model with an ecological niche model to disentangle the distinct and combined effects of forest loss and climate change.
Research sample	Our sample included a total of 5,882 occurrences of <i>V. variegata</i> and 95 of <i>V. rubra</i> .
Sampling strategy	Population sampling included two widely used distance sampling techniques, line transect surveys, rapid assessment surveys, capture-mark-resighting, and targeted behavioral observations. We sampled extensively from throughout the known extent of ruffed lemurs, including their northern and southernmost occurrences.
Data collection	Site records of detection/non-detection were obtained from field expeditions conducted by the authors between 1989 and 2017 throughout the known extent of ruffed lemurs (genus <i>Varecia</i> ). Population sampling included two widely used distance sampling techniques, line transect surveys, rapid assessment surveys, capture-mark-resighting, and targeted behavioral observations.
Timing and spatial scale	Site records of detection/non-detection were obtained from field expeditions conducted by the authors between 1989 and 2017, and occurred throughout the known extent of ruffed lemurs (genus <i>Varecia</i> ).
Data exclusions	All available detection localities were included in our study.
Reproducibility	We conducted all analyses using code primarily based on the <i>dismo</i> , <i>raster</i> , <i>geosphere</i> , and <i>rgeos</i> packages for the R Statistical Environment ver. 3.4.4113. The deforestation model also used the <i>phcfM50</i> and <i>fasterRaster</i> packages, the latter of which was linked to GRASS GIS 7.4.1115. Niche model construction and niche overlap procedures were conducted using the <i>enmSdm</i> package. All code is available at <a href="https://github.com/adamlilith/varecia">https://github.com/adamlilith/varecia</a> .
Randomization	We assessed overlap in the climatic niche of the two species using null model randomization tests based on the four climatic variables used in the niche modeling. Niche overlap was computed by comparing the occupancy of environmental space standardized by the frequency of available environmental space across species. Observed overlap was compared to a distribution of overlap values generated using a null model that randomizes the point locations across the study region. To generate the null models, we employed a flexible procedure based on the “rotate-translate-reflect” method to control for intra- and interspecific patterns in range geometry. We used the combined set of all randomized ranges across all iterations to represent the background (“available”) environment and computed niche overlap using Warren’s D and the Spearman rank-correlation coefficient.
Blinding	Blinding was not relevant to our study, as our study was not experimental by design. We used all detections of ruffed lemurs to generate species distribution models of the taxon.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	Fieldwork occurred throughout Madagascar's eastern rainforest corridor and spanned disturbance gradients ranging from well-established long-term study sites with extensive infrastructure to remote bushcamps lacking trail systems.
Location	Surveys occurred throughout Madagascar's eastern rainforest corridor, and included the known population extent of ruffed lemurs (genus <i>Varecia</i> ).
Access and import/export	Access to national parks was granted by ANGAP (Madagascar's National Park agency) and to protected areas by the Ministry of Forestry. Import/export of samples was not required for this study.
Disturbance	This study involved non-invasive observation methods.

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n/a	Involvement
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## Animals and other organisms

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Laboratory animals

The study did not involve laboratory animals

Wild animals

Site records of detection/non-detection were obtained from field expeditions conducted by the authors between 1989 and 2017. Population sampling included two widely used distance sampling techniques, line transect surveys, rapid assessment surveys, capture-mark-resighting, and targeted behavioral observations. All together we tallied 5882 occurrences of *V. variegata* and 95 of *V. rubra*. No animals were captured for this study

Field-collected samples

The study did not involve samples collected from the field

Ethics oversight

No ethics approval was required

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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