



RESEARCH ARTICLE

AMERICAN JOURNAL OF
PRIMATOLOGY WILEY

Do functional traits offset the effects of fragmentation? The case of large-bodied diurnal lemur species

Timothy M. Eppley^{1,2} | Luca Santini^{3,4} | Jen C. Tinsman^{5,6} | Giuseppe Donati⁷ ¹Institute for Conservation Research, San Diego Zoo Global, San Diego, California²Department of Anthropology, Portland State University, Portland, Oregon³Institute of Research on Terrestrial Ecosystems, National Research Council, Montelibretti, Italy⁴Department of Environmental Science, Faculty of Science, Institute for Wetland and Water Research, Radboud University, Nijmegen, The Netherlands⁵Institute of the Environment and Sustainability, University of California, Los Angeles, Los Angeles, California⁶Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York⁷Department of Social Sciences, Oxford Brookes University, Oxford, United Kingdom**Correspondence**Timothy M. Eppley, Institute for Conservation Research, San Diego Zoo Global, PO Box 120551, San Diego, CA 92112.
Email: TEppley@sandiegozoo.org**Abstract**

Primates worldwide are faced with increasing threats making them more vulnerable to extinction. Anthropogenic disturbances, such as habitat degradation and fragmentation, are among the main concerns, and in Madagascar, these issues have become widespread. As this situation continues to worsen, we sought to understand how fragmentation affects primate distribution throughout the island. Further, because species may exhibit different sensitivity to fragmentation, we also aimed to estimate the role of functional traits in mitigating their response. We collated data from 32 large-bodied lemur species ranges, consisting of species from the families Lemuridae (five genera) and Indriidae (two genera). We fitted Generalized Linear Models to determine the role of habitat fragmentation characteristics, for example, forest cover, patch size, edge density, and landscape configuration, as well as the protected area (PA) network, on the species relative probability of presence. We then assessed how the influence of functional traits (dietary guild, home range size) mitigate the response of species to these habitat metrics. Habitat area had a strong positive effect for many species, and there were significantly negative effects of fragmentation on the distribution of many lemur species. In addition, there was a positive influence of PAs on many lemur species' distribution. Functional trait classifications showed that lemurs of all dietary guilds are negatively affected by fragmentation; however, folivore-frugivores show greater flexibility/variability in terms of habitat area and landscape complexity compared to nearly exclusive folivores and frugivores. Furthermore, species of all home range sizes showed a negative response to fragmentation, while habitat area had an increasingly positive effect as home range increased in size. Overall, the general trends for the majority of lemur species are dire and point to the need for immediate actions on a multitude of fronts, most importantly landscape-level reforestation efforts.

KEYWORDS

habitat fragmentation, Indriidae, Lemuridae, Madagascar, species distribution

1 | INTRODUCTION

Tropical forests hold the majority of global biodiversity, yet these habitats are experiencing dramatic faunal declines due to continued threats from humans, a process now termed as “defaunation” (Dirzo

et al., 2014; Galetti et al., 2017; Gibson et al., 2013). Among these primary anthropogenic disturbances are habitat degradation and fragmentation, which can ultimately lead to local and widespread species extinctions via isolating small populations (Asner, Rudel, Aide, Defries, & Emerson, 2009; Dirzo et al., 2014; Gibson et al., 2011,

2013; Laurance et al., 2011; Tilman et al., 2017). Furthermore, fragments remaining within these human-modified landscapes are often considered unsuitable habitat for the majority of forest species (Laurance, Goosem, & Laurance, 2009). In fact, fragmentation results in extended edge habitats, which compared to normal forest interiors can be considered entirely distinct ecosystems (Laurance, Delamônica, Laurance, Vasconcelos, & Lovejoy, 2000; Pfeifer et al., 2017). Finally, forest fragmentation increases human accessibility to interior habitat, therefore, increasing the risk of illegal hunting (Benítez-López, Santini, Schipper, Busana, & Huijbregts, 2019). Taken together, increasingly anthropogenic landscapes have significant consequences on fauna populations (Ceballos, Ehrlich, & Dirzo, 2017; Dirzo et al., 2014).

Considering all primate species, more than half (approximately 60%) are threatened with extinction, with roughly 75% of all primate species experiencing declining population trends likely due to unsustainable human activities (Estrada et al., 2017). Madagascar is considered to be a biodiversity hotspot due to its many endemic species classified into the three IUCN Red List “threatened” categories, that is, critically endangered, endangered, and vulnerable (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Out of the 103 lemur species assessed by the IUCN in 2012, 20 were assessed as vulnerable, 49 as endangered, and 24 as critically endangered, making lemurs the most threatened vertebrate taxon (Schwitzer et al., 2013, 2014). The issues surrounding the decline of lemurs are myriad, with the reduction of lemur species richness primarily due to habitat loss through cultivation and timber harvesting (Ganzhorn, Lowry, Schatz, & Sommer, 2001; Ganzhorn, Wilmé, & Mercier, 2014; Hannah et al., 2008; Harper, Steininger, Tucker, Juhn, & Hawkins, 2007; Irwin et al., 2010; Schwitzer et al., 2014). Specifically, Madagascar's exponential population growth (UNFPA, 2017; World Bank, 2018) paired with a majority of the population living in extreme poverty in rural areas (World Bank, 2018), has increased pressure on the forests via human encroachment (Estrada et al., 2018).

Data from 2007 indicated that more than 80% of forested area in Madagascar falls within 1 km of the forest edge (Harper et al., 2007), while data from 2014 showed that the mean distance to forest edge on the island was approximately 300 m (Viellented et al., 2018). This trend will likely worsen as the human population of Madagascar continues to surge (UNFPA, 2017; World Bank, 2018). Fragmentation not only isolates populations by impeding animal dispersal and potential rescue effects on declining population and gene flow, but also worsens a number of additional threats (Fahrig, 2002). For example, increasing contact zones between anthropogenic and natural habitats contributes to increased zoonotic pathogen transmissions (Chapman, Gillespie, & Goldberg, 2005; Gortazar et al., 2014) and bushmeat hunting for subsistence (Golden, Bonds, Brashares, Rasolofoniaina, & Kremen, 2014; Razafimanahaka et al., 2012). The hunting of lemurs is illegal, but consumption of bushmeat in Madagascar is widespread, with poor rural households often targeting large diurnal lemur species (Borgerson, McKean, Sutherland, & Godfrey, 2016; Golden, 2009; Jenkins et al., 2011). Additionally, the

illegal pet trade has also been suggested to play a significant role in the reduction of wild populations (Reuter, Gilles, Wills, & Sewall, 2016), especially for some species, for example, *Lemur catta* (Gould & Sauther, 2016; LaFleur, Clarke, Reuter, & Schaefer, 2019).

Previous studies predicted that a majority of lemur species will experience massive range reductions, contracting the amount of habitat available to them (Brown & Yoder, 2015). Given that nearly all primate populations are declining due to anthropogenic disturbances (Estrada et al., 2017; Galán-Acedo, Arroyo-Rodríguez, Cudney-Valenzuela, & Fahrig, 2019a), it is imperative to understand specifically how lemurs are currently responding to habitat degradation, fragmentation, and forest loss. Patch-level approaches have been commonly applied to understand primate species' responses to habitat loss and fragmentation (Bodin & Norberg, 2007; Boyle & Smith, 2010; da Silva, Ribeiro, Hasui, da Costa, & da Cunha, 2015; Ganzhorn & Eisenbeiß, 2001; Schüßler, Radespiel, Ratsimbazafy, & Mantilla-Contreras, 2018; Steffens & Lehman, 2018), however, anthropogenic effects often occur at a landscape-level (Arroyo-Rodríguez & Fahrig, 2014; Arroyo-Rodríguez et al., 2013; Galán-Acedo, Arroyo-Rodríguez, Estrada, & Ramos-Fernández, 2019b; Galán-Acedo et al., 2019a). Due to the need for a landscape-level approach, we sought to determine how a number of habitat metrics influence the presence of all large-bodied diurnal/cathemeral primate species throughout Madagascar. We did not include nocturnal lemurs because (a) the taxonomy and distribution of nocturnal lemur species is poorly understood, with many species only known from a single location (e.g., see Hotaling et al., 2016; Lei et al., 2016), and (b), it has been shown that relatively smaller-bodied lemurs exhibit a greater tolerance to habitat fragmentation and disturbance compared to the larger-bodied diurnal/cathemeral species (Godfrey & Irwin, 2007). In fact, it has been shown that mammals of larger body mass are more sensitive to fragmentation and edge effects (Pfeifer et al., 2017). For these reasons, we modeled the role of various habitat characteristics on the presence of large-bodied diurnal/cathemeral species to understand how certain populations may be able to persist in the current landscape, including forest fragments, edges, and complex matrices. Given the critical state of human pressure on the remaining natural habitats of Madagascar, we predicted that all the lemurs considered will be negatively affected by anthropogenic disturbance.

It has been shown that species' responses to gradual and stochastic changes to environments may be mitigated by the species' functional traits (e.g., activity pattern, body size, dietary guild, home range size), and such an ability to expand niche breadth is vital to withstanding anthropogenic risks (Boyle & Smith, 2010; Donati et al., 2016; Eppley et al., 2017; Isaac & Cowlshaw, 2004; Lee, 2003; Nowak & Lee, 2013; Wiczowski, 2003). Unlike previous lemur-fragmentation studies that have only focused on site-specific or regional scales (e.g., Irwin et al., 2010; Kamilar & Tecot, 2016; Steffens & Lehman, 2018), the goal of our study was to model the role of two species functional traits (i.e., dietary guild, home range size) in determining sensitivity to fragmentation throughout Madagascar for all 32 large-bodied diurnal/cathemeral lemur species. As habitats

disappear, it has been postulated that dietary/habitat specialists will be affected more than dietary/habitat generalists, as high dietary diversity may buffer against extinction (Nowak & Lee, 2013). Frugivores are faced with a scattered spatial and temporal resource distribution, typically requiring extensive home ranges, potentially limiting their ability to cope within altered landscapes (Boyle & Smith, 2010; Campera et al., 2014; Donati et al., 2011; Estrada & Coates-Estrada, 1996; Rode, Chapman, McDowell, & Stickler, 2006). By comparison, folivores may be less affected by habitat degradation as leaves in secondary growth are often of higher dietary quality compared to those leaves available in mature forests (Chapman, Chapman, Bjorndal, & Onderdonk, 2002; Eppley, Donati, & Ganzhorn, 2016; Ganzhorn, 1995; Plumptre & Reynolds, 1994), though folivorous primates can be highly selective and potentially require equally large home ranges (Snaith & Chapman, 2005).

Specifically, considering the large-bodied lemurs, we made the following three predictions:

- (1) We expect lemur species with a high reliance on fruit resources and need for larger home ranges, such as *Varecia* and most *Eulemur*, to be severely affected by habitat availability and fragmentation.
- (2) We expect lemur species that are generalist folivores and utilize relatively smaller home ranges, for example, *Haplemur*, *Prolemur*, *Indri*, and some *Propithecus*, to be least affected by habitat availability and fragmentation.
- (3) We expect that lemurs with folivore-frugivore diets (e.g., *L. catta*, some *Eulemur* and some *Propithecus*) to display intermediate effects due to fragmentation metrics.

2 | METHODS

2.1 | Data collection

We obtained occurrence points for all diurnal and cathemeral lemur species, totaling 32 taxa, from the data set collated by Tinsman (2019). These include the genera *Eulemur* (12 species), *L. catta*, *Haplemur* (four species), *Prolemur simus*, and *Varecia* (two species/three subspecies) from the family Lemuridae, and *Propithecus* (nine species) and *Indri indri* from the family Indriidae. We considered the three *Varecia variegata* subspecies as separate taxa within our analyses as they are geographically isolated from one another and inhabit regions with differing degrees of pressure on the remaining forest habitat. The only species from these genera to be excluded was *Haplemur alaotrensis* as it is only known from the marsh areas surrounding Lac Alaotra (Rendigs, Reibelt, Ralainasolo, Ratsimbazafy, & Waeber, 2015), thus we did not have enough distribution points to allow for comprehensive modeling. Three types of sources were utilized: (a) points collected in the field by coauthors, (b) online databases including the Global Biodiversity Information Facility, Mammal Networked Information System, VertNet, Madagascar Lemurs Portal, and Réseau de la Biodiversité de Madagascar

(ReBioMa), and (c) peer-reviewed published sources. For this last source, we searched all articles published in *Lemur News*, *Madagascar Conservation and Development*, and *Primate Conservation* for GPS coordinates, in addition to several Google Scholar searches using a combination of various key terms. This yielded a total of 6,503 occurrence points across all forest types of various degrees of fragmentation in both protected and unprotected sites. Occurrence points were then vetted in which localities >50 km outside the species' IUCN occurrence area, as well as undated localities for species that have since been taxonomically split, were considered suspect and thus removed from the data set. Further, we only retained one occurrence point per 1-km cell. We were left with a remainder of 3,024 reliable and unique occurrence points (Figure S1). Data are available from the corresponding author upon request.

We obtained a 30-m resolution forest density map for 2010 from Vielledent et al. (2018) and binarized it at 75% of canopy coverage ($\geq 75\% = 1$; $< 75\% = 0$) consistently with what is done in Vielledent et al. (2018). Most of our occurrence data come from protected areas (PA) which are expected to be, on average, less fragmented and degraded; therefore, to avoid potential biases due to more frequent sampling in PAs, we also downloaded a spatial layer of the Madagascar Protected Area Network, hereafter referred to as PA, from the online database ReBioMa (Figure S2). Nearly all forests in Madagascar exhibit some relative degree of fragmentation (Vielledent et al., 2018), thus PA include both fragmented and less fragmented forests.

2.2 | Data preparation and fragmentation analysis

We used the binary forest maps (0 = nonforest; 1 = forest) to estimate the level of forest fragmentation at 1-km resolution. Many fragmentation metrics exist, partly because they measure different components of fragmentation, and partly because they measure these components using different approximations. Here we considered 11 different metrics (Table S1) and then used a principal component analysis (hereafter PCA) to reduce the factors considered within our model analysis. We used varimax rotation to improve interpretation of the PCA axes, and extracted the first three axes covering 95% of the total variance (Table S2). The first axis mostly accounted for the available habitat area (e.g., mean patch area, total core area, mean patch core area and proportion of canopy cover); the second axis mostly accounted for the actual fragmentation of the habitat (e.g., edge density, patch density, and perimeter area fractal dimension); and the third axis mostly accounted for landscape complexity (e.g., mean shape index, landscape shape index), that is, measuring the physical shape of the habitat (Tables 1 and S1). The first two axes, "habitat area" and "fragmentation," can be interpreted as the amount of habitat area per cell and the density of patches/edges per unit area, respectively. "Landscape complexity" can be interpreted as a measure of the overall geometric complexity of the landscape or of a focal class, in our case, forest. These indices are based on the ratio between perimeter and area and measure if patch

TABLE 1 Predictor variables included in the analyses.

	Interpretation	Description
Habitat metrics		
F1	Habitat area	Amount of habitat area per cell.
F2	Fragmentation	Density of patches or edges per unit area.
F3	Landscape complexity	Overall geometric complexity of the landscape. It measures if the shapes of patches tend to be simple and compact, or irregular and convoluted.
Protected areas		
PA	Used to control for the unbalanced sample of occurrence points inside and outside protected areas which may bias the estimated effect of fragmentation (generally higher outside PA).	Protected area network (1 = inside protected area; 0 = outside protected area).

Abbreviations: PA, protected areas.

shape tends to be simple and compact, or irregular and convoluted. It can also be interpreted as a measure of landscape disaggregation, where higher values indicate more dispersed patches in the landscape (McGarigal & Marks, 1995).

To test the influence of functional traits on species distribution, we assigned species according to their dietary guild. Previous authors have defined *frugivore* as an animal whose diet is composed of $\geq 50\%$ fruits (Donati et al., 2017; Fleming, Breitwisch, & Whitesides, 1987), and while this approach offers an easy solution, it overlooks the flexibility of some species that greatly shift their diet seasonally. Thus, we identified *folivore-frugivores* as species consuming between $\geq 35\%$ to $\leq 65\%$ fruit in their diet, with *frugivores* defined as $> 65\%$ fruit and *folivores* as $< 35\%$ fruit. This classification, though also crude, allows us to make meaningful comparisons between the three dietary guilds (Kappeler & Heymann, 1996). The diets of all lemur species were determined from a comprehensive literature survey using the All The World's Primates' (ATWP) database (Rowe & Myers, 2017). In the case of multiple behavioral and feeding ecology studies on a species, we calculated the mean percent of fruit consumed so as to have a single value. Of the lemurs included in the analyses, 11 species are considered folivores (*Haplemur* spp., *P. simus*, some *Propithecus* spp., and *Indri*), seven species are folivore-frugivores (some *Eulemur* spp., some *Propithecus* spp., and *L. catta*), while *Varecia* ssp. (four taxa) and most *Eulemur* spp. (nine taxa) maintain a frugivorous diet (Table S3). Additionally, we determined mean home range size (ha), hereafter referred to as "home range size," for each species following the same comprehensive literature survey via ATWP (Table S3; Rowe & Myers, 2017).

2.3 | Modeling

We tested for the effect of fragmentation on the species probability of presence using a species distribution modeling approach. For each species, we sampled a number of background (i.e., pseudo-absence) data points equal to 10 times the number of

presences (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). Background points are used to contrast the available habitat with the habitat where the species have been observed. When background points are used instead of real absences (i.e., presence-only models), the model estimates a relative probability of presence (Guillera-Arroita et al., 2015). Background points are commonly sampled randomly in areas potentially accessible to the species, often based on estimates of dispersal distance from occurrence points (e.g., Brown & Yoder, 2015; Thuiller, Lafourcade, Engler, & Araújo, 2009). Therefore, we limited the sampling of the randomly distributed background points within a buffer whose radius corresponded to the estimated dispersal distance of each species. Dispersal distance was estimated from home range areas using the allometric relationships in Santini et al. (2013). This ensured that we sampled background points only in areas potentially accessible to the species (Araújo et al., 2019). Background points falling in nonforested areas within the buffer were assigned the highest fragmentation values in the landscape. To control for the spatial bias and pseudo-replication of presence points, we only retained one presence point per 1-km, which exceeds the radius of home range area of all species in our sample (range = 0.06–0.65 km). To compare the strength of the relationship of different predictors, we standardized all predictor variables to a mean of 0 and a standard deviation of 1. Then, for each species we fitted a generalized linear model (GLM) with a binomial family, using the presences (1s) and background points (0s) as response variables, and the three fragmentation and the PA variables as predictors (Table 1). Including PA separately from the fragmentation axes allowed us to estimate the relative contribution of fragmentation to the relative probability of the presence of species while controlling for the confounding effect of PA. We ran a model selection for each of the models using AICc (Akaike Information Criterion corrected for small samples) and retained models with the lowest AICc value. Here we present the selected models and provide the full models within Supporting Information materials.

To test the effect of species traits on species sensitivity to fragmentation, we ran a generalized linear mixed-effect model (GLMM) including all species. We used the same predictors used in the single species GLM (F1, F2, F3, and PA) and the interaction between the three habitat metrics and the \log_{10} -transformed values of species average home range size and species dietary guild. We treated species as a random effect. We checked whether there was phylogenetic autocorrelation in the residuals and determined it was not necessary to control for phylogeny (Pagel Lambda = 0.300, $p = .103$).

All analyses were computed using R statistical software (R Core Team, 2017). We used the R package “psych” (Revelle, 2018) for the principal component analysis. We used the package “raster” (Hijmans & van Etten, 2014) for all raster operations and the package “sf” (Pebesma, 2018) for vector operations. We used “SDMTools” package (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014) to compute the fragmentation metrics, and “GISTools” (Brundson & Chen, 2014) to estimate the density kernel. This study adhered to the American Society of Primatology’s Principles for Ethical Treatment of Non-human Primates.

3 | RESULTS

In general, all habitat variables tested were important for most of the species (Figure 1 and Table S4), though five species, that is *Eulemur mongoz*, *Eulemur macaco*, *Propithecus deckenii*, *Propithecus coronatus*, and *Propithecus perrieri*, were not included in the selected models. The first habitat component (F1) accounting for habitat availability and mean patch area was significant in explaining the distribution of 10 taxa (31.3% of lemurs modeled). This F1 component had a positive effect on the distribution of these 10 species, mostly belonging to the genera *Eulemur* and *Propithecus*. The second component (F2) accounting for habitat fragmentation was significant in 14 taxa (43.8% of lemurs modeled), always showing a negative effect, therefore, indicating that for most species the probability of presence is lower when the habitat is fragmented. These fragmentation (F2) results equally affected at least some species of all genera, though *I. indri* was not included in this selected model. The third component (F3) accounting for landscape complexity was significant in 2 taxa (6.3% of lemurs modeled), negatively affecting the distribution of *Hapalemur occidentalis* and *V. v. subcincta* (Figure 1 and Table S4). Protected areas showed a positive effect in 37.5% of taxa modeled (Figure 1 and Table S4). Among species for which variables were not retained during model selection (i.e., the only-intercept model was the best model), there is also a pattern of a consistent negative effect of fragmentation (see Figure S3; Table S5 for full model results).

Considering the trait-specific analysis, the effect of a dietary guild on F1, all species regardless of diets were more likely to be present in areas with greater habitat availability and mean patch area (Figure 2a and Table S6). Regarding F2, all dietary guilds, that is, folivores, frugivores, and folivore-frugivores were negatively affected by the patch and edge density (Figure 2b and Table S6). The negative

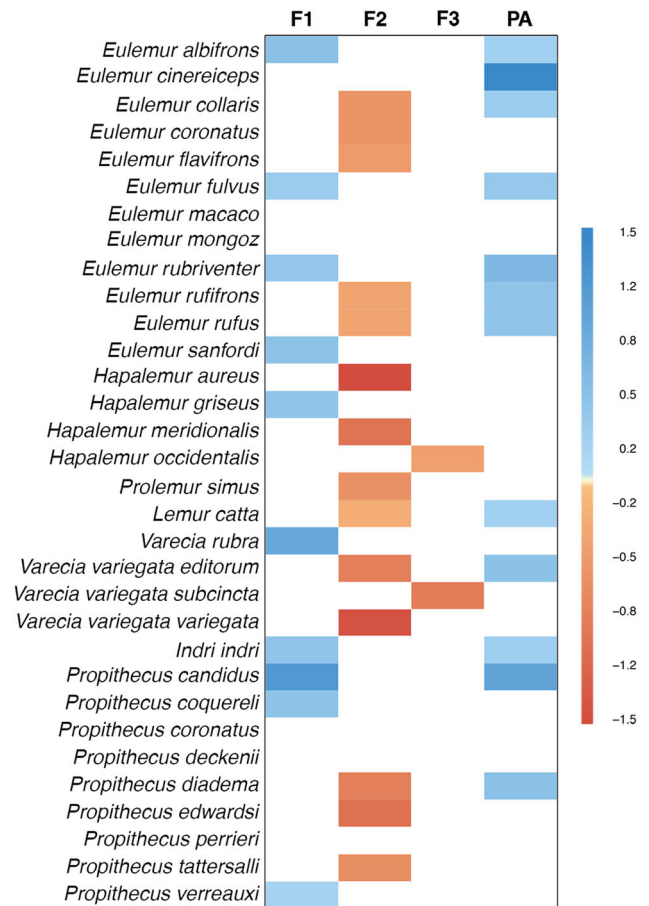


FIGURE 1 Heatmap showing the directional influence of various habitat metrics (F1: habitat area; F2: fragmentation; F3: landscape complexity) and PA metrics on the occurrence of diurnal and cathemeral lemur species belonging to the families Lemuridae and Indriidae. Empty boxes indicate variables that have been excluded after model selection. Species with no box are species for which the only-intercept model scored best. PA, protected area

effect of F2 became more strongly negative with increased home ranges of lemur species (Figure 3b and Table S6). Landscape complexity (F3) negatively affected both folivores and frugivores, while having a strong positive affect on folivore-frugivores (Figure 2c and Table S6). Finally, landscape complexity negatively affected species of both small and medium home range sizes, though positively affected species with large home range sizes (Figure 3c and Table S6).

4 | DISCUSSION

Among the three habitat variables considered (F1, F2, and F3), the one accounting for habitat fragmentation (F2; highly correlated with habitat patch and edge density) had the strongest overall negative effect on species distribution, while both F1 (habitat area) and PAs had strong positive effects on many species (Figure 1). On the contrary, landscape complexity does not appear to play a large role

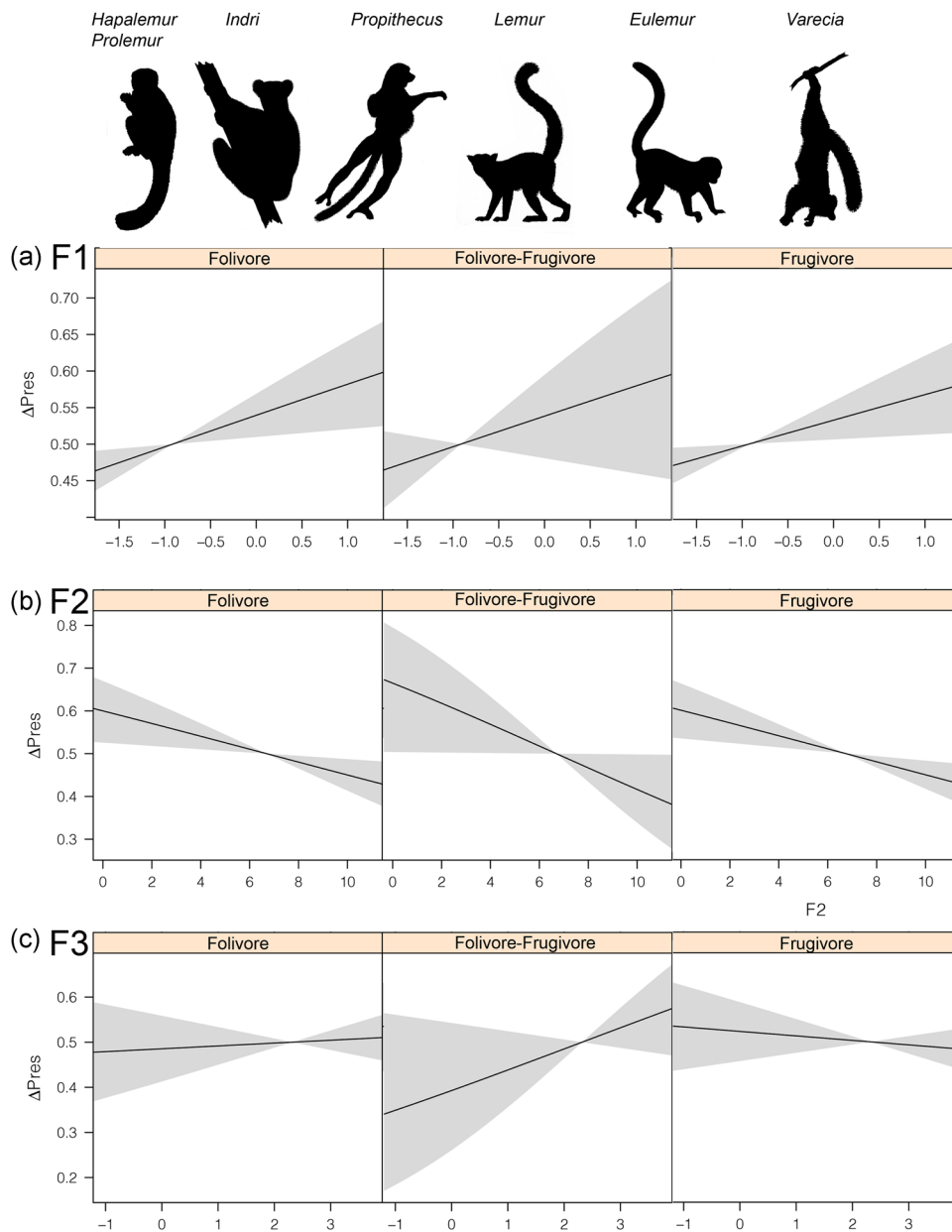


FIGURE 2 Partial responses by a dietary guild of the three habitat variables on the probability of lemur species occurrence. (a) F1: habitat area; (b) F2: fragmentation; and (c) F3: landscape complexity

affecting species distribution. Furthermore, as expected, species with larger home range areas were more negatively affected by habitat availability, but did not exhibit a higher sensitivity to fragmentation than species with small home range areas. Considering general trends, all dietary guilds were positively affected by F1 (habitat area) and negatively affected by F2 (fragmentation).

4.1 | True lemurs: *Eulemur* spp

Our analyses seem to mirror previously reported effects on the diverse *Eulemur* clade (Balestri et al., 2014; Bayart & Simmen, 2005; Brenneman et al., 2012; Campera et al., 2014; Donati et al., 2011;

Schwitzer, Randriatahina, Kaumanns, Hoffmeister, & Schwitzer, 2007; Tecot, 2013), with the distribution of many brown lemur species trending or significantly influenced by “habitat area” (F1) and “fragmentation” (F2). Habitat area positively affected the distribution of four, mostly rainforest inhabitant, *Eulemur* spp., including *Eulemur albifrons*, *Eulemur fulvus*, and *Eulemur rubriventer*. All three have large species ranges, though *Eulemur sanfordi* has a significantly smaller species range with less habitat available to it. Concerning F2, habitat fragmentation negatively or strongly negatively affected the distribution of five dry forest species, while landscape complexity (F3) provided no effects on *Eulemur* spp. distribution. In general terms, it appears that *Eulemur* species inhabiting larger, continuous humid forest tend to be more vulnerable to variations in canopy cover while

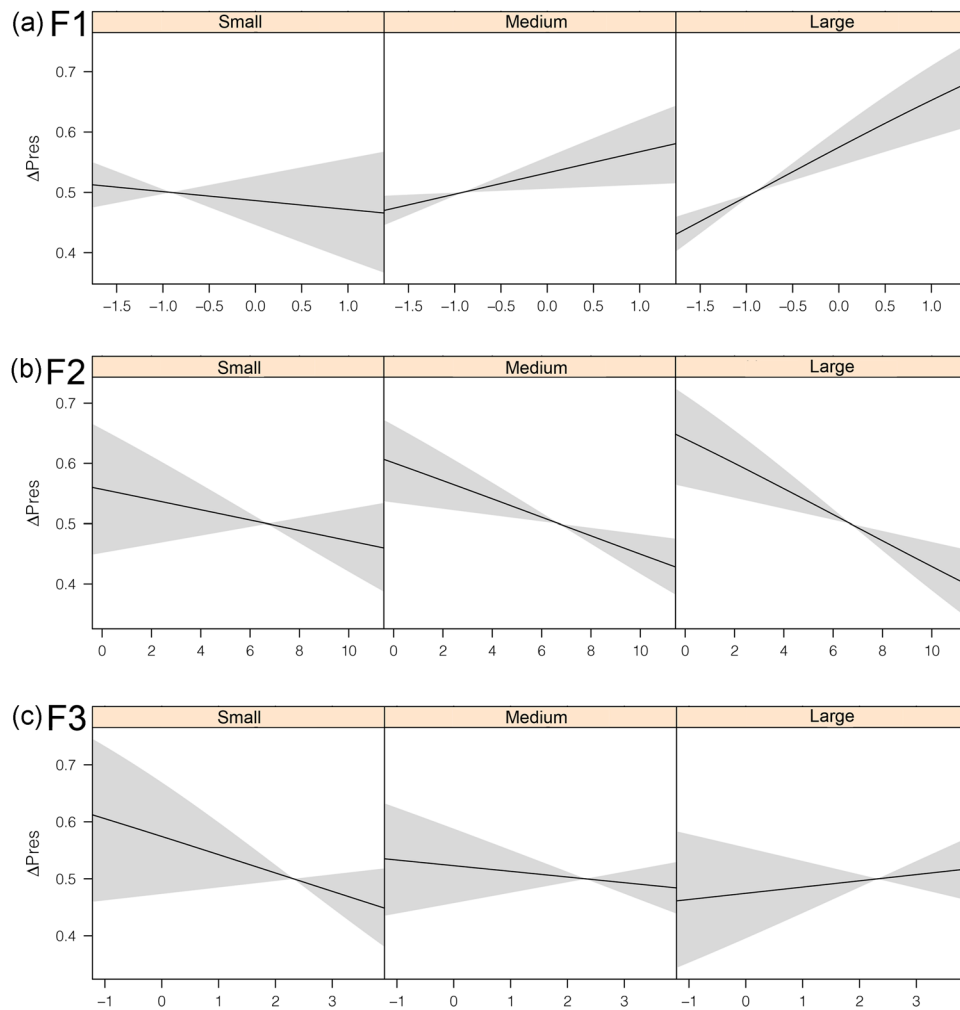


FIGURE 3 Partial responses of the three habitat variables on the probability of lemur species occurrence and their interaction with species average home range size. (a) F1: habitat area; (b) F2: fragmentation; and (c) F3: landscape complexity

species coping with more discontinuous and open dry forest habitat respond more to strict fragmentation and edge density. PAs showed a positive effect on the distribution of seven *Eulemur* spp., yet neither black lemurs (*Eulemur macaco*) nor mongoose lemurs (*Eulemur mongoz*) showed any effects to PA or the fragmentation metrics.

Overall, *Eulemur* taxa occur across all habitat types in Madagascar (Mittermeier et al., 2010). This genus consists of both frugivores and folivore-frugivores, and in addition to a relatively large dietary flexibility (but see Sato et al., 2016), they exhibit a wide variation in activity patterns (i.e., cathemerality), ranging pattern, and social organization (e.g., pair-living and multimale multifemale social groups), and as such, many species within are considered ecologically flexible primates (Donati, Bollen, Borgognini-Tarli, & Ganzhorn, 2007; Donati et al., 2011, 2016; Kappeler & Fichtel, 2016; Ossi & Kamilar, 2006; Overdorff, 1993a, 1993b; Sato et al., 2016). Smaller home-range requirements in western species compared to eastern species (Curtis & Zaramody, 1998; Donati et al., 2011; Donati, Lunardini, & Kappeler, 1999; Overdorff, 1993a; Sato et al., 2016; Schwitzer et al., 2007) and perhaps better abilities to cross the matrix between the

forest fragments (Steffens & Lehman, 2018) may allow them to persist despite the smaller available habitat area and reduced canopy cover. However, highly fragmented areas with significant edge effects still cause a negative response on the probability of occurrence of dry forest *Eulemur* suggesting a threshold of habitat degradation beyond which these flexible species disappear. In support of these negative effects of fragmentation, some *Eulemur* species living in relatively degraded habitats show clear signs of increased levels of stress (Balestri et al., 2014; Tecot, 2013).

4.2 | Ring-tailed lemurs: *L. catta*

Similar to some of the dry forest brown lemurs, our analysis revealed that ring-tailed lemurs (*L. catta*) were significantly affected by fragmentation. Considering the behavioral ecology of *L. catta*, it is not altogether surprising that the habitat and landscape complexity variables were not significant predictors. This geographically widespread species maintains a frugivorous-folivorous diet and is

considered the most ecologically flexible lemur and they have, in fact, been found in very small fragments, for example, <3 ha (Axel & Maurer, 2011; Cameron & Gould, 2013; Donati, Santini, Razafindramanana, Boitani, & Borgognini-Tarli, 2013; Gabriel, 2013; Goodman, Rakotoarisoa, & Wilmé, 2006; Gould, 2006; Gould & Andrianomena, 2015; Jolly, Koyama, & Rasamimanana, 2006; Kelley, 2011; LaFleur & Gould, 2009; Sauther, Sussman, & Gould, 1999). They are also semiterrestrial and known to exploit anthropogenic landscapes (Gabriel, 2013; LaFleur & Gould, 2009; Sauther et al., 2006), yet it is suggested that this species is sensitive to moderate habitat disturbance as populations occurring in poor quality habitats have lower densities (Gabriel, 2013; Kelley, 2011; Sussman, Green, Porton, Andrianasolondraibe, & Ratsirarson, 2003). Thus, their flexibility in being able to exploit areas outside of strict forest habitat at least allows this species to remain within fragmented landscapes in the short-term (Anderson, Rowcliffe, & Cowlishaw, 2007; Bodin, Tengö, Norman, Lundberg, & Elmqvist, 2006; Gabriel, 2013; Gould & Andrianomena, 2015). However, it is difficult to be optimistic about lemur persistence in increasingly fragmented and further isolated landscapes, which may lead to future genetic health bottlenecks (Parga, Sauther, Cuzzo, Jacky, & Lawler, 2012).

4.3 | Bamboo lemurs: *Haplemur* spp. and *Prolemur simus*

Fragmentation (F2) was more important than habitat availability (F1) and landscape complexity (F3) in determining the probability of presence of *Haplemur* species/*P. simus*. Bamboo lemurs are folivorous, and their ecological flexibility may allow bamboo lemurs to persist in heavily altered environments, allowing them to use edge habitat (Eppley et al., 2015, 2016, 2017; Grassi, 2006). Not all bamboo lemurs, however, are able to cope with habitat fragmentation. Similar to *Eulemur*, bamboo lemurs inhabiting large continuous areas (*Haplemur griseus*) appear more sensitive to habitat area (F1), while species inhabiting relatively smaller or more fragmented areas (i.e., *Haplemur aureus* and *Haplemur meridionalis*) are more sensitive to fragmentation (F2). In fact, *H. griseus* inhabits both humid and dry deciduous forest habitats (Mittermeier et al., 2010), which may be partially responsible for this contrast with other bamboo lemur species. The greater bamboo lemur (*P. simus*) used to be one of the most widespread lemur species (Godfrey, Jungers, Simons, Chatrath, & Rakotosamimanana, 1999), but is now restricted to a handful of sites within the eastern humid forests (Ravaloharimanitra et al., 2011; Wright et al., 2008). A recent study showed that its dwindling range was essentially the result of climate change altering botanical diversity within dry deciduous habitats, and causing the lemur's main food resource (giant bamboos) to go extinct locally (Eronen et al., 2017). For the most part, these areas are not yet formally protected by the government, but are being actively protected by both conservation research NGOs and local communities as they present an economic benefit to the surrounding area. In addition to these formally unprotected sites, the species is known to occur in Ranomafana

NP, while feeding remains have been observed in both Zahamena NP to the north, and Midongy du Sud NP in the south (Rakotonirina et al., 2011).

4.4 | Ruffed lemurs: *Varecia rubra* and *V. variegata* ssp

The various habitat metrics provided similar results across ruffed lemur taxa. Habitat area (F1) had a positive effect on *V. rubra* presence which inhabits the largest continuous humid forest remaining in Madagascar (Masoala-Makira) whereas fragmentation (F2) had a strongly negative effect on both *V. variegata editorum* and *V. v. variegata*. Taking into account the uneven distribution of this genus throughout its range, these findings are expected. Members of this genus are characterized by utilizing the largest relative food trees and maintaining large home ranges (Ratsimbazafy, 2006; Rigamonti, 1993; Vasey, 2000), to a degree that species densities are significantly lower and/or absent in anthropogenically impacted habitats leading to the perception that they are sensitive to habitat disturbance (Balko & Underwood, 2005; Herrera, Wright, Lauterbur, Ratavonjanahary, & Taylor, 2011; White, Overdorff, Balko, & Wright, 1995). Though generally true, some ruffed lemurs are known to inhabit less than ideal habitat, for example, shifting cultivation and secondary forest (Hekkala, Rakotondratsima, & Vasey, 2007), forest restoration zones (de Winter et al., 2018; Martinez & Razafindratsima, 2014), and even in degraded fragments intermixed with coffee plantations (Holmes et al., 2013), thus providing an explanation as to why *V. v. editorum* differs from the other ruffed lemurs. To build on this, however, it has been shown that patch size may influence how fast genetic diversity is lost after patch isolation (Holmes et al., 2013), with signs of genetic bottleneck occurring in degraded habitats (Razakamaharavo, McGuire, Vasey, Louis, & Breneman, 2010). With the current distribution occurring at low densities across fragmented populations (Baden et al., 2014; Holmes et al., 2013; Louis et al., 2005; Vasey, 2004), this threat may become even more dire following severe environmental disturbances, whether natural or anthropogenic. In fact, over a 10-year period (1991–2001), *V. v. editorum* within the small fragmented PA of Manombo Special Reserve failed to successfully reproduce (Ratsimbazafy, 2002), yet populations occurring at other sites were successful, thus the geographic coastal locale led to speculation that stochastic weather events resulted in low dietary quality foods (Dunham, Erhart, & Wright, 2010; Louis et al., 2005).

4.5 | Sifaka and indri: *Propithecus* spp. and *Indri indri*

Similar to bamboo lemurs, both habitat availability (F1) and fragmentation (F2) were important in determining the probability of presence of *Propithecus* spp. and *I. indri*. Sifaka (*Propithecus* spp.) are relatively widespread throughout most Madagascar habitats, that is, eastern humid, dry/humid deciduous, and spiny desert (Mittermeier

et al., 2010). For example, fragmentation had a strong negative effect on the distribution of golden-crowned sifaka (*Propithecus tattersalli*), a species endemic to the Daraina region of northern Madagascar (Quéméré, Amelot, Pierson, Crouau-Roy, & Chikhi, 2012). Interestingly, the distribution of Perrier's sifaka (*Propithecus perrieri*) a little further north of *P. tattersalli* showed no effects from any of the fragmentation metrics despite its current species range being quite fragmented. It is noted, however, that this species was able to disperse over large distances of open habitat within the recent past (Salmona et al., 2015). Habitat area (F1) positively affected both *Propithecus coquereli* and *Propithecus candidus*, two species whose populations are heavily concentrated in relatively large forest blocks in the west and east, respectively (Pichon et al., 2010; Salmona et al., 2014). Despite the widespread distribution, all *Propithecus* spp. are threatened by habitat loss from charcoal production and shifting cultivation (Kun-Rodrigues et al., 2014; Schwitzer et al., 2013).

Considering all nine sifaka species, both *Propithecus diadema* and *Propithecus verreauxi* inhabit the largest geographic areas, the central-northeastern humid forest and the dry deciduous/spiny desert of the southwest and far south, respectively (Mittermeier et al., 2010). The geographic range for *P. verreauxi* is among the largest of all lemurs, however, potentially four times larger than *P. diadema* (Mittermeier et al., 2010). Despite their widespread distribution, fragmentation (F2) negatively affected *P. diadema*, while habitat area (F1) positively affected *P. verreauxi*. These results are similar to other congeners (e.g., *Eulemur*) which inhabit distinctly different biomes, and is likely due to the large geographic range of *P. verreauxi*. At Berenty in the far south, *P. verreauxi* inhabits small degraded fragments that are associated with an abundance of protein-rich foods, potentially allowing this species to maintain relatively high densities (Norscia & Palagi, 2008). It should be noted that while *P. diadema* inhabit some fragmented forests, the long-term viability of these populations is unknown as previous research has suggested that smaller habitats can lead to morphometric signals of population decline (Irwin et al., 2019).

Habitat area (F1) had a significant effect on the largest extant lemur, indri (Junge, Barrett, & Yoder, 2011; Mittermeier et al., 2010). This species is restricted to the central-eastern humid forests (Mittermeier et al., 2010), yet despite their overall population sizes being reduced by habitat degradation, they display an ecological plasticity allowing them to live in various sized forest fragments (Glessner & Britt, 2005; Nunziata et al., 2016). However, this may be partially due to the significantly positive effect of PA on indri presence.

4.6 | Trait-specific sensitivity to fragmentation

Overall, lemurs' functional traits appear to be most affected by habitat availability and fragmentation as expected. Our models showed that greater habitat availability had a similar positive effect on both folivores and frugivores, thus species with these more specialized dietary preferences were more often distributed within larger habitat areas. While it is suggested that frugivores often have larger

home ranges to cope with the scattered spatial and temporal distribution of fruiting resources (Estrada & Coates-Estrada, 1996), folivores can be similarly highly selective of the leaves they consume and thus require larger habitat area (Snaith & Chapman, 2005). Considering folivore-frugivores, habitat area (F1) also had a positive effect though there appeared to be increased variability. It is possible that their flexible diet allows these species, for example, *Eulemur rufus*, *L. catta*, and *P. tattersalli* among others, to disproportionately inhabit smaller habitat patches and/or more open forests (Donati et al., 2011; Gould & Andrianomena, 2015; Irwin, 2008; Overdorff, 1993b). It is important to note that the diet of *Propithecus* is diverse and species are classified as either folivores or folivore-frugivores (Hemingway, 1998; Irwin, 2008; Koch, Ganzhorn, Rothman, Chapman, & Fichtel, 2017; Norscia, Carrai, & Borgognini-Tarli, 2006; Powzyk & Mowry, 2003; Sato et al., 2016), thus the folivore models may be more strongly influenced by other ecologically specialized lemurs, for example, bamboo lemurs and indri. Considering the mean sizes of home ranges, the effect of habitat area transitioned from negative to strongly positive as lemur home ranges increased, indicating that lemurs with small home ranges may prefer smaller habitat patches whereas species with large home range prefer large intact habitat areas.

The fragmentation metric (F2) had negative affect on species of all dietary guilds. This result was expected for frugivores which require larger habitat areas to meet their dietary demands, but it was unexpected for both folivore-frugivores and folivores which typically display a level of ecological flexibility allowing them to cope well within fragmented areas. In general, previous site-specific research has shown folivores to be less vulnerable to habitat disturbance and edge effects (Eppley et al., 2015, 2017; Ganzhorn, 1995; Lehman, Rajaonson, & Day, 2006), while frugivorous lemurs have been shown to be adversely affected by anthropogenic, degraded habitat (Balko & Underwood, 2005; Herrera et al., 2011; White et al., 1995). As frugivorous lemurs are important seed dispersers, they are essential for the maintenance of forest diversity and play a fundamental role in habitat regeneration (Federman et al., 2016; Ganzhorn, Fietz, Rakotavao, Schwab, & Zinner, 1999; Razafindratsima & Dunham, 2014; Wright et al., 2011). Folivore-frugivores, on the other hand, have previously showed mixed responses to edge habitats, possibly due to their wide dietary breadth across seasons, allowing some species to persist in degraded and fragmented landscapes (de Winter et al., 2018; Lehman et al., 2006; Sato et al., 2016). Yet, our overall results, however, show that each of these dietary guilds are near equally affected by fragmentation (F2). When considering lemur home range size, the effect of fragmentation became more strongly negative as home range size increased, as would be expected. Thus, species with smaller home ranges (e.g., *E. sanfordi*, *H. occidentalis*) are able to better cope with fragmentation compared to lemurs requiring large home ranges (e.g., *Varecia* spp.).

For the third habitat metric, landscape complexity (F3) showed a similar somewhat neutral effect on both folivores and frugivores. This is an unexpected result for lemurs with a folivorous diet, which often cope well within more fragmented habitat matrices (Boyle & Smith,

2010; Eppley et al., 2015). It should be noted that as exceptions, *H. occidentalis* (a folivore) and *V. v. subcincta* (a frugivore) showed significantly negative effects of landscape complexity. On the other hand, F3 displayed a strongly positive effect on folivore-frugivores meaning that their presence increased with landscape complexity. Similar to previous explanations for lemur folivore-frugivores, their flexible dietary ability potentially allows for them to locate resources in these habitats. Regardless of dietary guild, this habitat metric had a negative effect on lemurs across small and medium home range sizes, though a slightly positive effect on lemurs with large home ranges

4.7 | Potential caveats

In this study we made a number of assumptions to estimate the effect of habitat availability, fragmentation and complexity on the probability of species' presence. First, to apply fragmentation metrics, we had to binarize forest coverage, and used a threshold of 75% of canopy cover. While this seemed to be a reasonable threshold for most species (Vielledent et al., 2018), it may be too high for species selecting more open forest habitats such as ring-tailed lemurs. Second, we assumed species' presence to be an indication of habitat quality (intended as amount of habitat and its level of fragmentation), however this is a simplification as species may persist for a certain amount of time in a fragmented habitat (Araújo & Guisan, 2006; Chapman, Lawes, Naughton-Treves, & Gillespie, 2003). Therefore it is possible that the effects that we detected are diluted and thus, under-estimated. Third, we contrasted species' occurrence points with background points drawn randomly from the surrounding—potentially accessible—areas. If occurrence points were preferentially collected in more accessible areas (less dense and more fragmented forests) compared to more intact forest areas, our models may have estimated an inverse effect, as indicated with several *Eulemur* and *Haplemur* species within the full model (Table S5 and Figure S3). Fourth, it is possible that the positive effect of PAs is a genuine effect suggesting that species have a higher probability of occurrence in PAs than in surrounding areas; however, this may simply reflect the fact that most presence points are collected in PA. Finally, it is important to remember that while these models provide us with an interpretation for the current distribution of large-bodied lemurs throughout Madagascar, these data do not take into account exogenous factors (e.g., additional anthropogenic pressures, climate, etc.) that may be further impacting certain species and habitats. All in all, our results meet most of the expectations and show a consistent negative effect of fragmentation on species presence that is unlikely to arise from any of the above assumptions.

4.8 | Implications for conservation

The general trends for the majority of lemur species are dire and point to the need for immediate actions on a multitude of fronts.

These would require widespread implementation throughout Madagascar by actors at all levels if we hope to curtail the impending extinction of many lemur species. Among these actions are increasing landscape-level reforestation efforts. Implementing efforts to reduce deforestation rates while increasing reforestation efforts would help to prevent impending extinctions (Wearn, Reuman, & Ewers, 2012). Intrinsically, it is imperative to understand the responses of flora and fauna to natural and anthropogenic disturbance if we are to create effective restoration programs that increase forest buffer zones and corridors (Campera et al., 2014; Eppley et al., 2015, 2017; Hannah et al., 2008; Irwin et al., 2010; Kremen et al., 2008), and so more ground-level lemur population research is needed. Effectively, increasing fragment size may improve corridor connectivity potential within landscapes, and ultimately assist in species dispersal from source populations (Steffens & Lehman, 2018), thus increasing genetic diversity.

Also, maintaining permanent presence at field sites may reduce local anthropogenic pressures (e.g., hunting, timber harvesting) on species' populations as a consequence of providing consistent employment/direct benefits to local communities (Campera et al., 2019; Wrangham & Ross, 2008; Wright et al., 2012). Regardless of whether or not PAs are a legitimate predictor of species occurrence, a greater effort is needed to maintain park boundaries. Unfortunately, many park borders are being pushed farther back due to human encroachment from illegal timber harvesting and shifting cultivation practices (Allnutt, Asner, Golden, & Powell, 2013; Barrett, Brown, Morikawa, Labat, & Yoder, 2010). Even just considering Madagascar forests in general, the mean distance to edge has been estimated at 300 m, a number that is continuing to exponentially decrease (Vielledent et al., 2018).

While our results did show diverse responses by these lemur species to various habitat fragmentation metrics, this variance was likely dependent on species-specific ecological traits. Overall, our results support the critical need for further studies on dietary and habitat preferences, as well as life histories to further our understanding of how lemur species may respond to climatic and anthropogenic effects, especially forest loss and fragmentation.

ACKNOWLEDGMENTS

We would like to thank Lisa Gould for the invitation to present this study at the IPS symposium. Many thanks to Stephen Nash for providing us with silhouettes of his lemur artwork.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon request.

ORCID

Timothy M. Eppley  <http://orcid.org/0000-0003-1456-6948>

Luca Santini  <http://orcid.org/0000-0002-5418-3688>

Giuseppe Donati  <http://orcid.org/0000-0002-4803-0642>

REFERENCES

Allnutt, T. F., Asner, G. P., Golden, C. D., & Powell, G. V. (2013). Mapping recent deforestation and forest disturbance in northeastern

- Madagascar. *Tropical Conservation Science*, 6, 1–15. <https://doi.org/10.1177/194008291300600101>
- Anderson, J., Rowcliffe, J. M., & Cowlshaw, G. (2007). Does the matrix matter? A forest primate in a complex agricultural landscape. *Biological Conservation*, 135, 212–222. <https://doi.org/10.1016/j.biocon.2006.10.022>
- Araújo, M. B., Anderson, R. P., Barbosa, A. M., Beale, C. M., Dormann, C. F., Early, R., ... Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, 5, eaat4858. <https://doi.org/10.1126/sciadv.aat4858>
- Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33, 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>
- Arroyo-Rodríguez, V., Cuesta-del Moral, E., Mandujano, S., Chapman, C. A., Reyna-Hurtado, R., & Fahrig, L. (2013). Assessing habitat fragmentation effects on primates: The importance of evaluating questions at the correct scale. In L. Marsh & C. A. Chapman (Eds.), *Primates in fragments: Complexity and resilience* (pp. 13–28). New York, NY: Springer.
- Arroyo-Rodríguez, V., & Fahrig, L. (2014). Why is a landscape perspective important in studies of primates? *American Journal of Primatology*, 76, 901–909. <https://doi.org/10.1002/ajp.22282>
- Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R., & Emerson, R. (2009). A contemporary assessment of change in humid tropical forests. *Conservation Biology*, 23, 1386–1395. <https://doi.org/10.1111/j.1523-1739.2009.01333.x>
- Axel, A. C., & Maurer, B. A. (2011). Lemurs in a complex landscape: Mapping species density in subtropical dry forests of southwestern Madagascar using data at multiple levels. *American Journal of Primatology*, 73, 38–52. <https://doi.org/10.1002/ajp.20872>
- Baden, A. L., Holmes, S. M., Johnson, S. E., Engberg, S. E., Louis, E. E., Jr, & Bradley, B. J. (2014). Species-level view of population structure and gene flow for a critically endangered primate (*Varecia variegata*). *Ecology and Evolution*, 4, 2675–2692. <https://doi.org/10.1002/ece3.1119>
- Balestri, M., Barresi, M., Campera, M., Serra, V., Ramanamanjato, J. B., Heistermann, M., & Donati, G. (2014). Habitat degradation and seasonality affect physiological stress levels of *Eulemur collaris* in littoral forest fragments. *PLOS One*, 9, e107698. <https://doi.org/10.1371/journal.pone.0107698>
- Balko, E. A., & Underwood, H. B. (2005). Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Primatology*, 66, 45–70. <https://doi.org/10.1002/ajp.20127>
- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, 3, 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- Barrett, M. A., Brown, J. L., Morikawa, M. K., Labat, J.-N., & Yoder, A. D. (2010). CITES designation for endangered rosewood in Madagascar. *Science*, 328, 1109–1110. <https://doi.org/10.1126/science.1187740>
- Bayart, F., & Simmen, B. (2005). Demography, range use, and behavior in black lemurs (*Eulemur macaco macaco*) at Ampasikely, northwest Madagascar. *American Journal of Primatology*, 67, 299–312. <https://doi.org/10.1002/ajp.20186>
- Benítez-López, A., Santini, L., Schipper, A. M., Busana, M., & Huijbregts, M. A. J. (2019). Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLOS Biology*, 17, e300024. <https://doi.org/10.1371/journal.pbio.3000247>
- Bodin, Ö., & Norberg, J. (2007). A network approach for analyzing spatially structured populations in fragmented landscape. *Landscape Ecology*, 22, 31–44. <https://doi.org/10.1007/s10980-006-9015-0>
- Bodin, Ö., Tengö, M., Norman, A., Lundberg, J., & Elmqvist, T. (2006). The value of small size: Loss of forest patches and ecological thresholds in southern Madagascar. *Ecological Applications*, 16, 440–451. [https://doi.org/10.1890/1051-0761\(2006\)016\[0440:TVOSSL\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0440:TVOSSL]2.0.CO;2)
- Borgerson, C., McKean, M. A., Sutherland, M. R., & Godfrey, L. R. (2016). Who hunts lemurs and why they hunt them. *Biological Conservation*, 197, 124–130. <https://doi.org/10.1016/j.biocon.2016.02.012>
- Boyle, S. A., & Smith, A. T. (2010). Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? *Biological Conservation*, 143, 1134–1143. <https://doi.org/10.1016/j.biocon.2010.02.008>
- Brenneman, R. A., Johnson, S. E., Bailey, C. A., Ingraldi, C., Delmore, K. E., Wyman, T. M., ... Louis, E. E. (2012). Population genetics and abundance of the Endangered grey-headed lemur *Eulemur cinereiceps* in south-east Madagascar: Assessing risks for fragmented and continuous populations. *Oryx*, 46, 298–307. <https://doi.org/10.1017/S0030605311000159>
- Brown, J. L., & Yoder, A. D. (2015). Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution*, 5, 1131–1142. <https://doi.org/10.1002/ece3.1418>
- Brundson, C., & Chen, H. (2014). GISTools: Some further GIS capabilities for R. R package version 0.7-4. Retrieved from <https://CRAN.R-project.org/package=GISTools>
- Cameron, A., & Gould, L. (2013). Fragment adaptive behavioural strategies and inter-site variation in the ring-tailed lemur (*Lemur catta*) at Anja Special Reserve and the Tsaranoro Valley, southcentral Madagascar. In L. Marsh & C. A. Chapman (Eds.), *Primates in fragments: Complexity and resilience* (pp. 227–243). New York, NY: Springer.
- Campera, M., Phelps, M., Besnard, F., Balestri, M., Eppley, T. M., Nijman, V., & Donati, G. (2019). Forest management and researchers' presence reduced hunting and forest exploitation by local communities in Tsitongambarika, Madagascar. *Oryx*, 53, 677–686. <https://doi.org/10.1017/S0030605317001211>
- Campera, M., Serra, V., Balestri, M., Barresi, M., Ravaolahy, M., Randriatafika, F., & Donati, G. (2014). Effects of habitat quality and seasonality on ranging patterns of collared brown lemur (*Eulemur collaris*) in littoral forest fragments. *International Journal of Primatology*, 35, 957–975. <https://doi.org/10.1007/s10764-014-9780-6>
- Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>
- Chapman, C. A., Chapman, L. J., Bjorndal, K., & Onderdonk, D. A. (2002). Application of protein to fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology*, 23, 283–310. <https://doi.org/10.1023/A:1013831511405>
- Chapman, C. A., Gillespie, T. R., & Goldberg, T. L. (2005). Primates and the ecology of their infectious diseases: How will anthropogenic change affect host-parasite interactions? *Evolutionary Anthropology*, 14, 134–144. <https://doi.org/10.1002/evan.20068>
- Chapman, C. A., Lawes, M. J., Naughton-Treves, L., & Gillespie, T. (2003). Primate survival in community-owned forest fragments: Are metapopulation models useful amidst intensive use? In L. K. Marsh (Ed.), *Primates in fragments: Ecology and conservation* (pp. 63–78). New York, NY: Kluwer Academic/Plenum Publishers.
- Curtis, D. J., & Zaramody, A. (1998). Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. *International Journal of Primatology*, 19, 811–835. <https://doi.org/10.1023/A:1020341312735>
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406. <https://doi.org/10.1126/science.1251817>
- Donati, G., Bollen, A., Borgognini-Tarli, S. M., & Ganzhorn, J. U. (2007). Feeding over the 24-h cycle: Dietary flexibility of cathemeral collared lemurs (*Eulemur collaris*). *Behavioral Ecology and Sociobiology*, 61, 1237–1251. <https://doi.org/10.1007/s00265-007-0354-x>

- Donati, G., Campera, M., Balestri, M., Serra, V., Barresi, M., Schwitzer, C., ... Santini, L. (2016). Ecological and anthropogenic correlates of activity patterns in *Eulemur*. *International Journal of Primatology*, 37, 29–46. <https://doi.org/10.1007/s10764-015-9876-7>
- Donati, G., Kesch, K., Ndremitfy, K., Schmidt, S. L., Ramanamanjato, J. B., Borgognini-Tarli, S. M., & Ganzhorn, J. U. (2011). Better few than hungry: Flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. *PLOS One*, 6, e19807. <https://doi.org/10.1371/journal.pone.0019807>
- Donati, G., Lunardini, A., & Kappeler, P. M. (1999). Cathemeral activity of red-fronted brown lemurs (*Eulemur fulvus rufus*) in the Kirindy Forest/CFPF. In B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn & S. M. Goodman (Eds.), *New directions in lemur studies* (pp. 119–137). Boston, MA: Springer.
- Donati, G., Santini, L., Eppley, T. M., Arrigo-Nelson, S. J., Balestri, M., Boinski, S., ... Ganzhorn, J. U. (2017). Low levels of fruit nitrogen as drivers for the evolution of Madagascar's primate communities. *Scientific Reports*, 7, 14406. <https://doi.org/10.1038/s41598-017-13906-y>
- Donati, G., Santini, L., Razafindramanana, J., Boitani, L., & Borgognini-Tarli, S. (2013). Un-expected nocturnal activity in "Diurnal" *Lemur catta* supports cathemerality as one of the key adaptations of the lemurid radiation. *American Journal of Physical Anthropology*, 150, 99–106. <https://doi.org/10.1002/ajpa.22180>
- Dunham, A. E., Erhart, E. M., & Wright, P. C. (2010). Global climate cycles and cyclones: Consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology*, 17, 219–227. <https://doi.org/10.1111/j.1365-2486.2010.02205.x>
- Eppley, T. M., Balestri, M., Campera, M., Rabenantoandro, J., Ramanamanjato, J.-B., Randriatafika, F., ... Donati, G. (2017). Ecological flexibility as measured by the use of pioneer and exotic plants by two lemurids: *Eulemur collaris* and *Haplemur meridionalis*. *International Journal of Primatology*, 38, 338–357. <https://doi.org/10.1007/s10764-016-9943-8>
- Eppley, T. M., Donati, G., & Ganzhorn, J. U. (2016). Determinants of terrestrial feeding in an arboreal primate: The case of the southern bamboo lemur (*Haplemur meridionalis*). *American Journal of Physical Anthropology*, 161, 328–342. <https://doi.org/10.1002/ajpa.23034>
- Eppley, T. M., Donati, G., Ramanamanjato, J.-B., Randriatafika, F., Andriamandimbarisoa, L. N., Ravelomanantsoa, R., & Ganzhorn, J. U. (2015). The use of an invasive species habitat by a small folivorous primate: Implications for conservation. *PLOS One*, 10, e0140981. <https://doi.org/10.1371/journal.pone.0140981>
- Eronen, J. T., Zohdy, S., Evans, A. R., Tecot, S. R., Wright, P. C., & Jernvall, J. (2017). Feeding ecology and morphology make a bamboo specialist vulnerable to climate change. *Current Biology*, 27, 3384–3389. <https://doi.org/10.1016/j.cub.2017.09.050>
- Estrada, A., & Coates-Estrada, R. (1996). Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas. *International Journal of Primatology*, 5, 759–783. <https://doi.org/10.1007/BF02735263>
- Estrada, A., Garber, P. A., Mittermeier, R. A., Wich, S., Gouveia, S., Dobrovolski, R., ... Setiawan, A. (2018). Primates in peril: The significance of Brazil, Madagascar, Indonesia and the Democratic Republic of the Congo for global primate conservation. *PeerJ*, 6, e4869. <https://doi.org/10.7717/peerj.4869>
- Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., ... Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3, e1600946. <https://doi.org/10.1126/sciadv.1600946>
- Fahrig, L. (2002). Effect of habitat fragmentation on the extinction threshold: A synthesis. *Ecological Applications*, 12, 346–353. [https://doi.org/10.1890/1051-0761\(2002\)012\[0346:EOHFOT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0346:EOHFOT]2.0.CO;2)
- Federman, S., Dornburg, A., Daly, D. C., Downie, A., Perry, G. H., Yoder, A. D., ... Baden, A. L. (2016). Implications of lemuriform extinctions for the Malagasy flora. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 5041–5046. <https://doi.org/10.1073/pnas.1523825113>
- Fleming, T. H., Breitwisch, R., & Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology, Evolution, and Systematics*, 18, 91–109. <https://doi.org/10.1146/annurev.es.18.110187.000515>
- Gabriel, D. N. (2013). Habitat use and activity patterns as an indication of fragment quality in a strepsirrhine primate. *International Journal of Primatology*, 34, 388–406. <https://doi.org/10.1007/s10764-013-9668-x>
- Galetti, M., Brocardo, C. R., Begotti, R. A., Hortenci, L., Rocha-Mendes, F., Bernardo, C. S. S., ... Siqueira, T. (2017). Defaunation and biomass collapse of mammals in the largest Atlantic forest remnant. *Animal Conservation*, 20, 270–281. <https://doi.org/10.1111/acv.12311>
- Galán-Acedo, C., Arroyo-Rodríguez, V., Cudney-Valenzuela, S. J., & Fahrig, L. (2019a). A global assessment of primate responses to landscape structure. *Biological Reviews*, 94, 1605–1618. <https://doi.org/10.1111/brv.12517>
- Galán-Acedo, C., Arroyo-Rodríguez, V., Estrada, A., & Ramos-Fernández, G. (2019b). Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. *Landscape Ecology*, 34, 147–158. <https://doi.org/10.1007/s10980-018-0753-6>
- Ganzhorn, J. U. (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*, 76, 2084–2096. <https://doi.org/10.2307/1941683>
- Ganzhorn, J. U., & Eisenbeiß, B. (2001). The the concept of nested species assemblages and its utility for understanding effects of habitat fragmentation. *Basic and Applied Ecology*, 2, 87–99. <https://doi.org/10.1078/1439-1791-00040>
- Ganzhorn, J. U., Fietz, J., Rakotovo, E., Schwab, D., & Zinner, D. (1999). Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*, 13, 794–804. <https://doi.org/10.1046/j.1523-1739.1999.98245.x>
- Ganzhorn, J. U., Lowry, P. P., Schatz, G. E., & Sommer, S. (2001). The biodiversity of Madagascar: One of the world's hottest hotspots on its way out. *Oryx*, 35, 346–348. <https://doi.org/10.1046/j.1365-3008.2001.00201.x>
- Ganzhorn, J. U., Wilmé, L., & Mercier, J.-L. (2014). Explaining Madagascar's biodiversity. In I. R. Scales (Ed.), *Conservation and environmental management in Madagascar* (pp. 17–43). New York, NY: Routledge.
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., ... Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–381. <https://doi.org/10.1038/nature10425>
- Gibson, L., Lynam, A. J., Bradshaw, C. J., He, F., Bickford, D. P., Woodruff, D. S., ... Laurance, W. F. (2013). Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, 341, 1508–1510. <https://doi.org/10.1126/science.1240495>
- Glessner, K. D., & Britt, A. (2005). Population density and home range size of *Indri indri* in a protected low altitude rain forest. *International Journal of Primatology*, 26, 855–872. <https://doi.org/10.1007/s10764-005-5326-2>
- Godfrey, L. R., & Irwin, M. T. (2007). The evolution of extinction risk: Past and present anthropogenic impacts on the primate communities of Madagascar. *Folia Primatologica*, 78, 405–419. <https://doi.org/10.1159/000105152>
- Godfrey, L. R., Jungers, W. L., Simons, E. L., Chatrath, P. S., & Rakotosamimanana, B. (1999). Past and present distributions of lemurs in Madagascar. In B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn & S. M. Goodman (Eds.), *New directions in lemur studies* (pp. 19–53). Boston, MA: Springer.

- Golden, C. D. (2009). Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: A conservation and livelihoods issue. *Oryx*, 43, 386–392. <https://doi.org/10.1017/S0030605309000131>
- Golden, C. D., Bonds, M. H., Brashares, J. S., Rasolofoniaina, B. J. R., & Kremen, C. (2014). Economic valuation of subsistence harvest of wildlife in Madagascar. *Conservation Biology*, 28, 234–243. <https://doi.org/10.1111/cobi.12174>
- Goodman, S. M., Rakotoarisoa, S. V., & Wilmé, L. (2006). The distribution and biogeography of the ring-tailed lemur (*Lemur catta*) in Madagascar. In A. Jolly, R. W. Sussman, N. Koyama & H. Rasamimanana (Eds.), *Ringtailed lemur biology* (pp. 3–15). New York, NY: Springer.
- Gortazar, C., Reperant, L. A., Kuiken, T., de la Fuente, J., Boadella, M., Martínez-Lopez, B., ... Mysterud, A. (2014). Crossing the interspecies barrier: Opening the door to zoonotic pathogens. *PLOS Pathogens*, 10, e1004129. <https://doi.org/10.1371/journal.ppat.1004129>
- Gould, L., & Andrianomena, P. (2015). Ring-tailed lemurs (*Lemur catta*), forest fragments, and community-level conservation in south-central Madagascar. *Primate Conservation*, 29, 67–74. <https://doi.org/10.1896/052.029.0108>
- Gould, L. (2006). *Lemur catta* ecology: What we know and what we need to know. In L. Gould & M. L. Sauther (Eds.), *Lemurs: Ecology and adaptation* (pp. 255–274). New York, NY: Springer.
- Gould, L., & Sauther, M. L. (2016). Going, going, gone... Is the iconic ring-tailed lemur (*Lemur catta*) headed for imminent extirpation. *Primate Conservation*, 30, 89–101.
- Grassi, C. (2006). Variability in habitat, diet, and social structure of *Haplemur griseus* in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, 131, 50–63. <https://doi.org/10.1002/ajpa.20423>
- Guillera-Arroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A., Kujala, H., Lentini, P. E., ... Wintle, B. A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography*, 24, 276–292. <https://doi.org/10.1111/geb.12268>
- Hannah, L., Dave, R., Lowry, P. P., II, Andelman, S., Andrianarisata, M., Andriamaro, L., ... Wilmé, L. (2008). Climate change adaptation for conservation in Madagascar. *Biology Letters*, 4, 590–594. <https://doi.org/10.1098/rsbl.2008.0270>
- Harper, G. J., Steiner, M. K., Tucker, C. J., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, 34, 325–333. <https://doi.org/10.1017/S0376892907004262>
- Hekkala, E. R., Rakotondratsima, M., & Vasey, N. (2007). Habitat and distribution of the ruffed lemur, *Varecia*, north of the Bay of Antongil in northeastern Madagascar. *Primate Conservation*, 22, 88–95. <https://doi.org/10.1896/052.022.0107>
- Hemingway, C. A. (1998). Selectivity and variability in the diet of Milne-Edwards' sifakas (*Propithecus diadema edwardsi*): Implications for folivory and seed-eating. *International Journal of Primatology*, 19, 355–377. <https://doi.org/10.1023/A:1020344018670>
- Herrera, J. P., Wright, P. C., Lauterbur, E., Ratavonjanahary, L., & Taylor, L. L. (2011). The effects of habitat disturbance on lemurs at Ranomafana National Park. *International Journal of Primatology*, 32, 1091–1108. <https://doi.org/10.1007/s10764-011-9525-8>
- Hijmans, R. J., & van Etten, J. (2014). raster: Geographic data analysis and modeling. *R Package Version*, 2(8). Retrieved from <http://cran.r2056project.org/package=raster>
- Holmes, S. M., Baden, A. L., Brenneman, R. A., Engberg, S. E., Louis, E. E., & Johnson, S. E. (2013). Patch size and isolation influence genetic patterns in black-and-white ruffed lemur (*Varecia variegata*) populations. *Conservation Genetics*, 14, 615–624. <https://doi.org/10.1007/s10592-013-0455-1>
- Hotaling, S., Foley, M. E., Lawrence, N. M., Bocanegra, J., Blanco, M. B., Rasoloarison, R., ... Weisrock, D. W. (2016). Species discovery and validation in a cryptic radiation of endangered primates: Coalescent-based species delimitation in Madagascar's mouse lemurs. *Molecular Ecology*, 25, 2029–2045. <https://doi.org/10.1111/mec.13604>
- Irwin, M. T. (2008). Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. *International Journal of Primatology*, 29, 95–115. <https://doi.org/10.1007/s10764-007-9222-9>
- Irwin, M. T., Samonds, K. E., Raharison, J. L., Junge, R. E., Mahefarisoa, K. L., Rasambainarivo, F., ... Glander, K. E. (2019). Morphometric signals of population decline in diademed sifakas occupying degraded rainforest habitat in Madagascar. *Scientific Reports*, 9, 8776. <https://doi.org/10.1038/s41598-019-45426-2>
- Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., ... Ganzhorn, J. U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation*, 143, 2351–2362. <https://doi.org/10.1016/j.biocon.2010.01.023>
- Isaac, N. J., & Cowlshaw, G. (2004). How species respond to multiple extinction threats. *Proceedings of the Royal Society of London B: Biological Sciences*, 271, 1135–1141. <https://doi.org/10.1098/rspb.2004.2724>
- Jenkins, R. K. B., Keane, A., Rakotoarivelo, A. R., Rakotomboavonjy, V., Randrianandrianina, F. H., Razafimanahaka, H. J., ... Jones, J. P. G. (2011). Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLOS One*, 6, e27570. <https://doi.org/10.1371/journal.pone.0027570>
- Jolly, A., Koyama, N., & Rasamimanana, H. (2006). *Ringtailed lemur biology*. New York, NY: Springer.
- Junge, R. E., Barrett, M. A., & Yoder, A. D. (2011). Effects of anthropogenic disturbance on indri (*Indri indri*) health in Madagascar. *American Journal of Primatology*, 73, 632–642. <https://doi.org/10.1002/ajp.20938>
- Kamilar, J. M., & Tecot, S. R. (2016). Anthropogenic and climatic effects on the distribution of *Eulemur* species: An ecological niche modeling approach. *International Journal of Primatology*, 37, 47–68. <https://doi.org/10.1007/s10764-015-9875-8>
- Kappeler, P. M., & Fichtel, C. (2016). The evolution of *Eulemur* social organization. *International Journal of Primatology*, 37, 10–28. <https://doi.org/10.1007/s10764-015-9873-x>
- Kappeler, P. M., & Heymann, E. W. (1996). Nonconvergence in the evolution of primate life history and socio-ecology. *Biological Journal of the Linnean Society*, 59, 297–326. <https://doi.org/10.1111/j.1095-8312.1996.tb01468.x>
- Kelley, E. A. (2011). Lemur catta in the region of Cap Sainte-Marie, Madagascar: Introduced cacti, xerophytic Didiereaceae-Euphorbia bush, and tombs (Unpublished doctoral dissertation). Washington University, St. Louis.
- Koch, F., Ganzhorn, J. U., Rothman, J. M., Chapman, C. A., & Fichtel, C. (2017). Sex and seasonal differences in diet and nutrient intake in Verreaux's sifakas (*Propithecus verreauxi*). *American Journal of Primatology*, 79, 1–10. <https://doi.org/10.1002/ajp.22595>
- Kremen, C., Cameron, A., Moilanen, A., Phillips, S. J., Thomas, C. D., Beentje, H., ... Zjhra, M. L. (2008). Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science*, 320, 222–226. <https://doi.org/10.1126/science.1155193>
- Kun-Rodrigues, C., Salmona, J., Besolo, A., Rasolondraibe, E., Rabarivola, C., Marques, T. A., ... Chikhi, L. (2014). New density estimates of a threatened sifaka species (*Propithecus coquereli*) in Ankarafantsika National Park. *American Journal of Primatology*, 76, 515–528. <https://doi.org/10.1002/ajp.22243>
- LaFleur, M., Clarke, T. A., Reuter, K. E., & Schaefer, M. S. (2019). Illegal trade of wild-captured *Lemur catta* within Madagascar. *Folia Primatologica*, 90, 199–214. <https://doi.org/10.1159/000496970>
- LaFleur, M., & Gould, L. (2009). Feeding outside the forest: The importance of crop raiding and an invasive weed in the diet of

- gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*, 80, 233–246. <https://doi.org/10.1159/000240968>
- Laurance, W. F., Camargo, J. L., Luizão, R. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., ... Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, 144, 56–67. <https://doi.org/10.1016/j.biocon.2010.09.021>
- Laurance, W. F., Delamônica, P., Laurance, S. G., Vasconcelos, H. L., & Lovejoy, T. E. (2000). Rainforest fragmentation kills big trees. *Nature*, 404, 836. <https://doi.org/10.1038/35009032>
- Laurance, W. F., Goosem, M., & Laurance, S. G. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, 24, 659–669. <https://doi.org/10.1016/j.tree.2009.06.009>
- Lee, P. C. (2003). Innovation as a behavioural response to environmental challenges: A cost and benefit approach. In S. M. Reader (Ed.), *Animal innovation* (pp. 261–276). Oxford: Oxford University Press.
- Lehman, S. M., Rajaonson, A., & Day, S. (2006). Edge effects and their influence on lemur density and distribution in southeast Madagascar. *American Journal of Physical Anthropology*, 129, 232–241. <https://doi.org/10.1002/ajpa.20241>
- Lei, R., Frasier, C. L., Hawkins, M. T., Engberg, S. E., Bailey, C. A., Johnson, S. E., ... Louis, E. E. (2016). Phylogenomic reconstruction of sportive lemurs (genus *Lepilemur*) recovered from mitogenomes with inferences for Madagascar biogeography. *Journal of Heredity*, 108, 107–119. <https://doi.org/10.1093/jhered/esw072>
- Louis, E. E., Ratsimbazafy, J. H., Razakamaharau, V. R., Pierson, D. J., Barber, R. C., & Brenneman, R. A. (2005). Conservation genetics of black and white ruffed lemurs, *Varecia variegata*, from Southeastern Madagascar. *Animal Conservation*, 8, 105–111. <https://doi.org/10.1017/S1367943004001891>
- Martinez, B. T., & Razafindratsima, O. H. (2014). Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a forest restoration site in Masoala National Park, Madagascar. *Folia Primatologica*, 85, 228–243. <https://doi.org/10.1159/000363408>
- McGarigal, K., & Marks, B. J. (1995). *FRAGSTATS: spatial pattern analysis program for quantifying landscape structure* (Gen. Tech. Rep. PNW-GTR-351). Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 122p, 351.
- Mittermeier, R. A., Louis, E. E., Jr, Richardson, M., Schwitzer, C., Langrand, O., Rylands, A. B., ... Mackinnon, J. (2010). *Lemurs of Madagascar* (3rd ed.). Washington, DC: Conservation International.
- 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. <https://doi.org/10.1038/35002501>
- Norscia, I., Carrai, V., & Borgognini-Tarli, S. M. (2006). Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *International Journal of Primatology*, 27, 1001–1022. <https://doi.org/10.1007/s10764-006-9056-x>
- Norscia, I., & Palagi, E. (2008). Berenty 2006: Census of *Propithecus verreauxi* and possible evidence of population stress. *International Journal of Primatology*, 29, 1099–1115. <https://doi.org/10.1007/s10764-008-9259-4>
- Nowak, K., & Lee, P. C. (2013). “Specialist” primates can be flexible in response to habitat alteration. In L. K. Marsh & C. A. Chapman (Eds.), *Primates in fragments: Complexity and resilience*. Developments in Primatology: Progress and Prospects (pp. 199–211). New York, NY: Springer Science+Business Media.
- Nunziata, S. O., Wallenhorst, P., Barrett, M. A., Junge, R. E., Yoder, A. D., & Weisrock, D. W. (2016). Population and conservation genetics in an Endangered lemur, *Indri indri*, across three forest reserves in Madagascar. *International Journal of Primatology*, 37, 688–702. <https://doi.org/10.1007/s10764-016-9932-y>
- Ossi, K. M., & Kamilar, J. M. (2006). Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemuridae). *Behavioral Ecology and Sociobiology*, 61, 53–64. <https://doi.org/10.1007/s00265-006-0236-7>
- Overdorff, D. J. (1993b). Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *International Journal of Primatology*, 14, 721–753. <https://doi.org/10.1007/BF02192188>
- Overdorff, D. J. (1993a). Ecological and reproductive correlates to range use in red-bellied lemurs (*Eulemur rubriventer*) and rufous lemurs (*Eulemur fulvus rufus*). In P. M. Kappeler & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 167–178). Boston, MA: Springer.
- Parga, J. A., Sautther, M. L., Cuozzo, F. P., Jacky, I. A. Y., & Lawler, R. R. (2012). Evaluating ring-tailed lemurs (*Lemur catta*) from southwestern Madagascar for a genetic population bottleneck. *American Journal of Physical Anthropology*, 147, 21–29. <https://doi.org/10.1002/ajpa.21603>
- Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, 10, 439–446.
- Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., ... Ewers, R. M. (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, 551, 187. <https://doi.org/10.1038/nature24457>
- Pichon, C., Tarnaud, L., Bayart, F., Hladik, A., Hladik, C. M., & Simmen, B. (2010). Feeding ecology of the crowned sifaka (*Propithecus coronatus*) in a coastal dry forest in northwest Madagascar (SFUM, Antrema). *Lemur News*, 15, 43–47.
- Plumptre, A. J., & Reynolds, V. (1994). The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology*, 31, 631–641. <https://doi.org/10.2307/2404154>
- Powzyk, J. A., & Mowry, C. B. (2003). Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *International Journal of Primatology*, 24, 1143–1162. <https://doi.org/10.1023/B:IJOP.0000005984.36518.94>
- Quéméré, E., Amelot, X., Pierson, J., Crouau-Roy, B., & Chikhi, L. (2012). Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 13028–13033. <https://doi.org/10.1073/pnas.1200153109>
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.Rproject.org>
- Rakotonirina, L., Rajaonson, A., Ratolojanahary, T., Rafalimandimby, J., Fanomezantsoa, P., Ramahefasoa, B., ... King, T. (2011). New distributional records and conservation implications for the critically endangered greater bamboo lemur *Prolemur simus*. *Folia Primatologica*, 82, 118–129. <https://doi.org/10.1159/000330910>
- Ratsimbazafy, J. (2002). On the brink of extinction and the process of recovery: responses of black-and-white ruffed lemurs (*Varecia variegata variegata*) to disturbance in Manombo forest, Madagascar (Unpublished doctoral dissertation). SUNY-Stony Brook.
- Ratsimbazafy, J. (2006). Diet composition, foraging, and feeding behavior in relation to habitat disturbance: Implications for the adaptability of ruffed lemurs (*Varecia variegata*) in Manombo Forest. In L. Gould & M. L. Sautther (Eds.), *Lemurs: Ecology and adaptation* (pp. 403–422). New York, NY: Springer.
- Ravaloharimanitra, M., Ratolojanahary, T., Rafalimandimby, J., Rajaonson, A., Rakotonirina, L., Rasolofoharivelo, T., ... King, T. (2011). Gathering local knowledge in Madagascar results in a major increase in the known range and number of sites for critically endangered greater bamboo lemurs (*Prolemur simus*). *International Journal of Primatology*, 32, 776–792. <https://doi.org/10.1007/s10764-011-9500-4>
- Razafimanahaka, J. H., Jenkins, R. K. B., Andriafidison, D., Randrianandrianina, F., Rakotomboavonjy, V., Keane, A., &

- Jones, J. P. G. (2012). Novel approach for quantifying illegal bushmeat consumption reveals high consumption of protected species in Madagascar. *Oryx*, 46, 584–592. <https://doi.org/10.1017/S0030605312000579>
- Razafindratsima, O. H., & Dunham, A. E. (2014). Assessing the impacts of nonrandom seed dispersal by multiple frugivore partners on plant recruitment. *Ecology*, 96, 24–30. <https://doi.org/10.1890/14-0684.1>
- Razakamiharavo, V. R., McGuire, S. M., Vasey, N., Louis, E. E., & Brenneman, R. A. (2010). Genetic architecture of two red ruffed lemur (*Varecia rubra*) populations of Masoala National Park. *Primates*, 51, 53–61. <https://doi.org/10.1007/s10329-009-0171-0>
- Rendigs, A., Reibelt, L. M., Ralainasolo, F. B., Ratsimbazafy, J. H., & Waeber, P. O. (2015). Ten years into the marshes—*Hapalemur alaotrensis* conservation, one step forward and two steps back? *Madagascar Conservation & Development*, 10, 13–20. <https://doi.org/10.4314/mcd.v10i1.S3>
- Reuter, K. E., Gilles, H., Wills, A. R., & Sewall, B. J. (2016). Live capture and ownership of lemurs in Madagascar: Extent and conservation implications. *Oryx*, 50, 344–354. <https://doi.org/10.1017/S003060531400074X>
- Revelle, W. (2018). Psych: Procedures for personality and psychological research, Northwestern University, Evanston. R package version 1.8.12. Retrieved from <https://CRAN.R-project.org/package=psych>
- Rigamonti, M. M. (1993). Home range and diet in red ruffed lemurs (*Varecia variegata rubra*) on the Masoala Peninsula, Madagascar. In P. M. Kappeler & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 25–39). Boston, MA: Plenum Press.
- Rode, K. D., Chapman, C. A., McDowell, L. R., & Stickler, C. (2006). Nutritional correlates of population density across habitats and logging intensities in redbell monkeys (*Cercopithecus ascanius*). *Biotropica*, 38, 625–634. <https://doi.org/10.1111/j.1744-7429.2006.00183.x>
- Rowe, N., & Myers, M. (2017). *All the World's primates*. Charlestown, RI: Primate Conservation, Inc. Retrieved from <http://www.alltheworldsprimates.org>
- Salmona, J., Jan, F., Rasolondraibe, E., Besolo, A., Oussen, D. S., Beck, A., ... Chikhi, L. (2014). Extensive survey of the Endangered Coquerel's sifaka *Propithecus coquereli*. *Endangered Species Research*, 25, 175–183. <https://doi.org/10.3354/esr00622>
- Salmona, J., Teixeira, H., Rasolondraibe, E., Aleixo-Pais, I., Kun-Rodriguez, C., Rakotonanahary, A. N., ... Chikhi, L. (2015). Genetic diversity, population size, and conservation of the Critically Endangered Perrier's sifaka (*Propithecus perrieri*). *International Journal of Primatology*, 36, 1132–1153. <https://doi.org/10.1007/s10764-015-9881-x>
- Santini, L., Di Marco, M., Visconti, P., Baisero, D., Boitani, L., & Rondinini, C. (2013). Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix*, 24, 181–186. <https://doi.org/10.4404/hystrix-24.2-8746>
- Sato, H., Santini, L., Patel, E. R., Campera, M., Yamashita, N., Colquhoun, I. C., & Donati, G. (2016). Dietary flexibility and feeding strategies of *Eulemur*: A comparison with *Propithecus*. *International Journal of Primatology*, 37, 109–129. <https://doi.org/10.1007/s10764-015-9877-6>
- Sauther, M. L., Fish, K. D., Cuozzo, F. P., Miller, D. S., Hunter-Ishikawa, M., & Culbertson, H. (2006). Patterns of health, disease, and behavior among wild ringtailed lemurs, *Lemur catta*: Effects of habitat and sex. In A. Jolly, R. W. Sussman, N. Koyama & H. Rasamimanana (Eds.), *Ringtailed lemur biology: Lemur catta in Madagascar* (pp. 313–331). New York, NY: Springer.
- Sauther, M. L., Sussman, R. W., & Gould, L. (1999). The socioecology of the ringtailed lemur: Thirty-five years of research. *Evolutionary Anthropology: Issues, News, and Reviews*, 8, 120–132. [https://doi.org/10.1002/\(SICI\)1520-6505\(1999\)8:4<120::AID-EVAN3>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1520-6505(1999)8:4<120::AID-EVAN3>3.0.CO;2-O)
- Schüßler, D., Radespiel, U., Ratsimbazafy, J. H., & Mantilla-Contreras, J. (2018). Lemurs in a dying forest: Factors influencing lemur diversity and distribution in forest remnants of north-eastern Madagascar. *Biological Conservation*, 228, 17–26. <https://doi.org/10.1016/j.biocon.2018.10.008>
- Schwitzer, C., Mittermeier, R. A., Davies, N., Johnson, S., Ratsimbazafy, J., Razafindramanana, J., Louis, E. E., Jr, & Rajaobelina, S. (2013). *Lemurs of Madagascar: A strategy for their conservation 2013–2016*. Bristol, UK: IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International.
- Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., ... Wright, P. C. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, 343, 842–843. <https://doi.org/10.1126/science.1245783>
- Schwitzer, N., Randriatahina, G. H., Kaumanns, W., Hoffmeister, D., & Schwitzer, C. (2007). Habitat utilization of blue-eyed black lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in primary and altered forest fragments. *Primate Conservation*, 22, 79–87. <https://doi.org/10.1896/052.022.0106>
- da Silva, L. G., Ribeiro, M. C., Hasui, E., da Costa, C. A., & da Cunha, R. G. T. (2015). Patch size, functional isolation, visibility and matrix permeability influences Neotropical primate occurrence within highly fragmented landscapes. *PLOS One*, 10, e0114025. <https://doi.org/10.1371/journal.pone.0114025>
- Snaith, T. V., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: Patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Ptilocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, 59, 185–190. <https://doi.org/10.1007/s00265-005-0023-x>
- Steffens, T. S., & Lehman, S. M. (2018). Lemur species-specific metapopulation responses to habitat loss and fragmentation. *PLOS One*, 13, e0195791. <https://doi.org/10.1371/journal.pone.0195791>
- Sussman, R. W., Green, G., Porton, I., Andrianasolondraibe, O. L., & Ratsirarson, J. (2003). A survey of the habitat of *Lemur catta* in southwestern and southern Madagascar. *Primate Conservation*, 19, 32–52.
- Tecot, S. (2013). Variable energetic strategies in disturbed and undisturbed rain forest habitats: Fecal cortisol levels in southeastern Madagascar. In J. Masters, M. Gamba, F. Génin & R. Tuttle (Eds.), *Leaping ahead: Advances in prosimian biology* (pp. 185–195). New York, NY: Springer.
- Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography*, 32, 369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>
- Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, 546, 73–81. <https://doi.org/10.1038/nature22900>
- Tinsman, J. C. (2019). Geospatial and genomic tools for conserving the Critically Endangered blue-eyed black lemur (*Eulemur flavifrons*) and the sportive lemurs (genus *Lepilemur*) (Unpublished doctoral dissertation). Columbia University.
- UNFPA. (2017). *The State of World Population 2017: Worlds Apart—Reproductive Health and Rights in an Age of Inequality*. New York, NY.
- VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L., & Storlie, C. (2014). SDMTTools: Species distribution modelling tools: Tools for processing data associated with species distribution modelling exercises. R package version, 1, 1–221. Retrieved from <http://cran.r-project.org/package=SDMTTools>
- Vasey, N. (2000). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *American Journal of Physical Anthropology*, 112, 411–431. [https://doi.org/10.1002/1096-8644\(200007\)112:3<411::AID-AJPA10>3.0.CO;2-R](https://doi.org/10.1002/1096-8644(200007)112:3<411::AID-AJPA10>3.0.CO;2-R)
- Vasey, N. (2004). *Varecia*, ruffed lemurs. In S. M. Goodman & J. P. Benstead (Eds.), *The natural history of Madagascar* (pp. 1332–1336). Chicago, IL: The University of Chicago Press.
- Vielledent, 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. *Biological Conservation*, 222, 189–197. <https://doi.org/10.1016/j.biocon.2018.04.008>
- Wearn, O. R., Reuman, D. C., & Ewers, R. M. (2012). Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science*, 337, 228–232. <https://doi.org/10.1126/science.1219013>
- White, F. J., Overdorff, D. J., Balko, E. A., & Wright, P. C. (1995). Distribution of ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. *Folia Primatologica*, 64, 124–131. <https://doi.org/10.1159/000156842>
- Wieczkowski, J. A. (2003). Aspects of the ecological flexibility of the Tana River mangabey (*Cercocebus galeritus*) in its fragmented habitat, Tana River, Kenya (Unpublished doctoral dissertation). University of Georgia.
- de Winter, I., van der Hoek, S., Schütt, J., Heitkönig, I. M., Van Hooft, P., Gort, G., ... Sterck, F. (2018). Anthropogenic disturbance effects remain visible in forest structure, but not in lemur abundances. *Biological Conservation*, 225, 106–116. <https://doi.org/10.1016/j.biocon.2018.03.021>
- World Bank. (2018). Poverty and shared prosperity 2018: Piecing together the poverty puzzle, Washington, DC: World Bank.
- Wrangham, R., & Ross, E. (2008). *Science and conservation in African forests: The benefit of long-term research*. Cambridge: Cambridge University Press.
- Wright, P. C., Erhart, E. M., Tecot, S., Baden, A. L., Arrigo-Nelson, S. J., Herrera, J., ... Zohdy, S. (2012). Long-term lemur research at Centre Valbio, Ranomafana National Park, Madagascar. In P. M. Kappeler & D. P. Watts (Eds.), *Long-term field studies of primates* (pp. 67–100). Berlin, Heidelberg: Springer.
- Wright, P. C., Johnson, S. E., Irwin, M. T., Jacobs, R., Schlichting, P., Lehman, S., ... Razafindratsita, V. (2008). The crisis of the critically endangered greater bamboo lemur (*Prolemur simus*). *Primate Conservation*, 23, 5–18. <https://doi.org/10.1896/052.023.0102>
- Wright, P. C., Tecot, S. R., Erhart, E. M., Baden, A. L., King, S. J., & Grassi, C. (2011). Frugivory in four sympatric lemurs: Implications for the future of Madagascar's forests. *American Journal of Primatology*, 73, 585–602. <https://doi.org/10.1002/ajp.20936>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Eppley TM, Santini L, Tinsman JC, Donati G. Do functional traits offset the effects of fragmentation? The case of large-bodied diurnal lemur species. *Am J Primatol*. 2020;82:e23104. <https://doi.org/10.1002/ajp.23104>