RESEARCH ARTICLE

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

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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, Delamô-nica, 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 to-gether, increasingly anthropogenic landscapes have significant con-sequences 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 un-sustainable 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" cate-gories, 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 as-sessed as vulnerable, 49 as endangered, and 24 as critically en-dangered, 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 har-vesting (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 encroach-ment (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 (Vielledent et al., 2018). This trend will likely worsen as the human population of Madagascar continues to surge (UNFPA, 2017; World Bank, 2018). Fragmenta-tion 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 ex-ample, 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 tar-geting 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 dis-turbances (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' re-sponses 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 noc-turnal 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 ex-hibit 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 sto-chastic 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 & Cowlishaw, 2004; Lee, 2003; Nowak & Lee, 2013; Wieczkowski, 2003). Unlike previous lemur-fragmentation studies that have only focused on site-specific or re-gional 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 de-termining 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, *Hapalemur*, *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*, *Hapalemur* (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 *Hapalemur 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 Reseau 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 (≥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.	Positively related with the proportion of forest, patch aggregation and mean patch area.
F2	Fragmentation	Density of patches or edges per unit area.	Positively related to patch density and edge density.
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.	Positively related to landscape shape index and mean shape index.
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 ≥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 ≥35% to ≤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 (*Hapalemur* spp., *P. simus*, some *Propithecus* spp., and *Indri*), seven 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 (1 s) and background points (0 s) 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
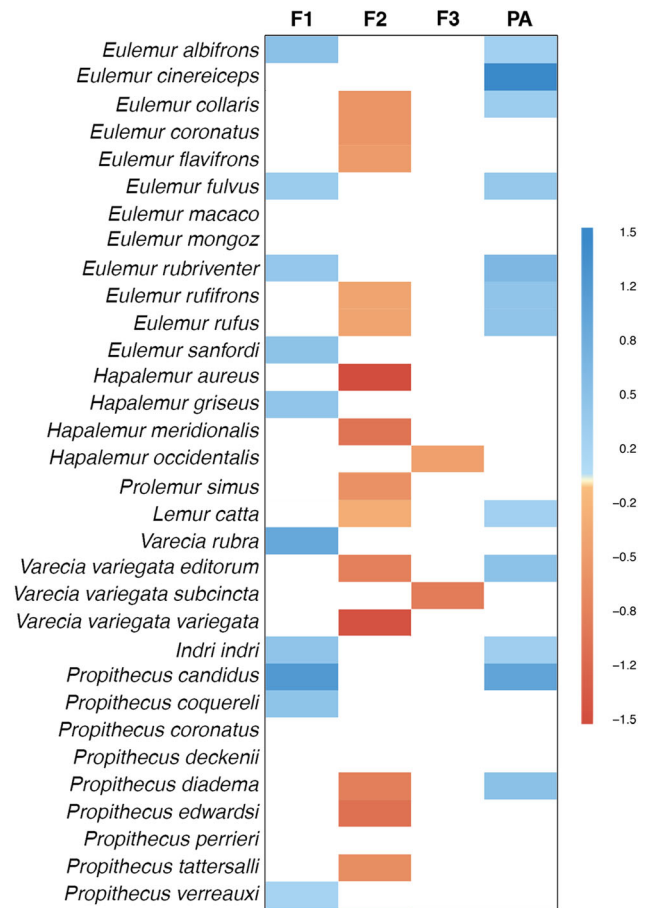

FIGURE 1 Heatmap showing the directional influence of various habitat metrics (F1: habitat area; F2: fragmentation; F3: landscape complexity) and PA metrics on the occurrence of diurnal and cathemeral lemur species belonging to the families Lemuridae and Indriidae. Empty boxes indicate variables that 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
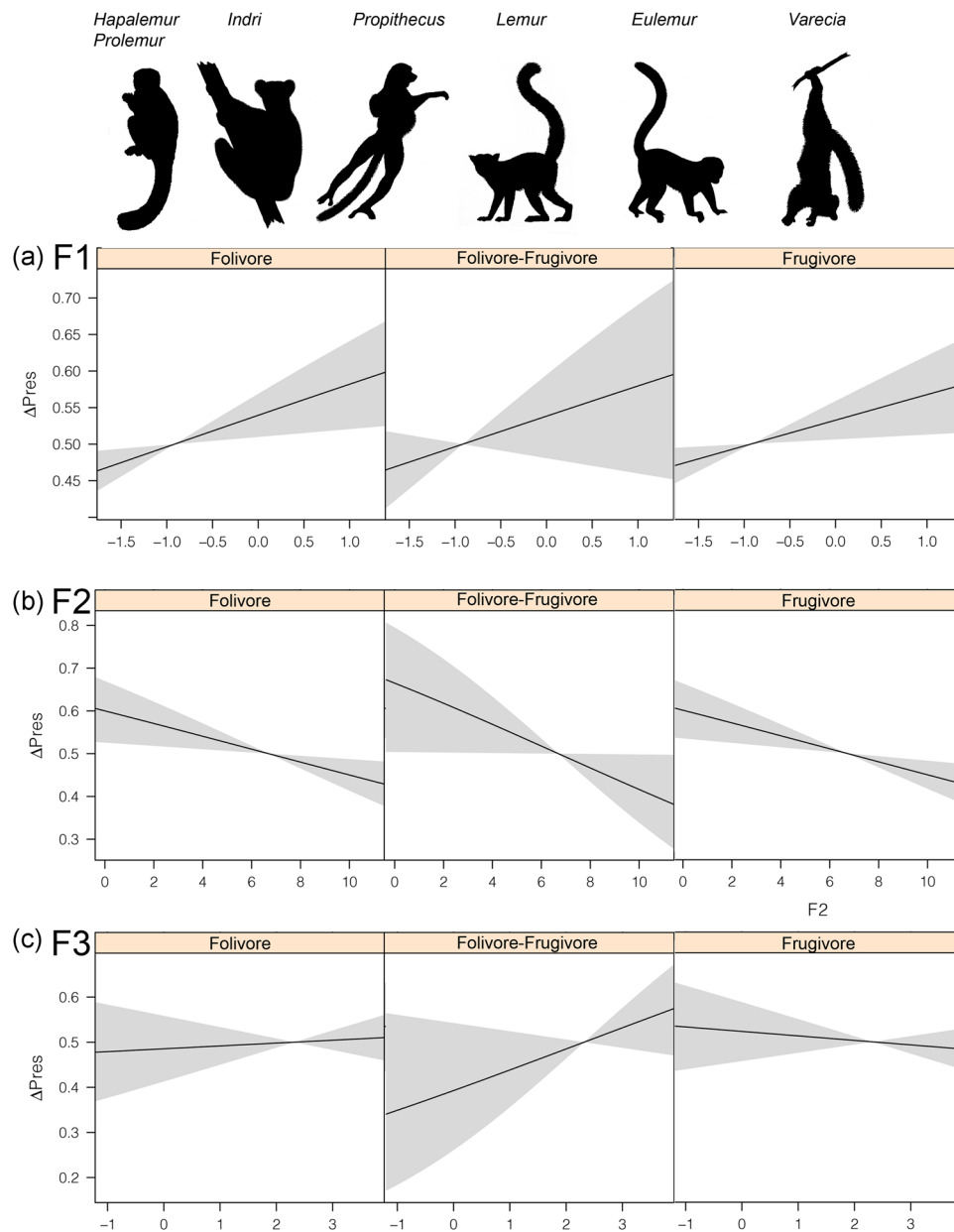
FIGURE 2 Partial responses by a dietary guild of the three habitat variables on the probability of lemur species occurrence. (a) F1: habitat area; (b) F2: fragmentation; and (c) F3: landscape complexity

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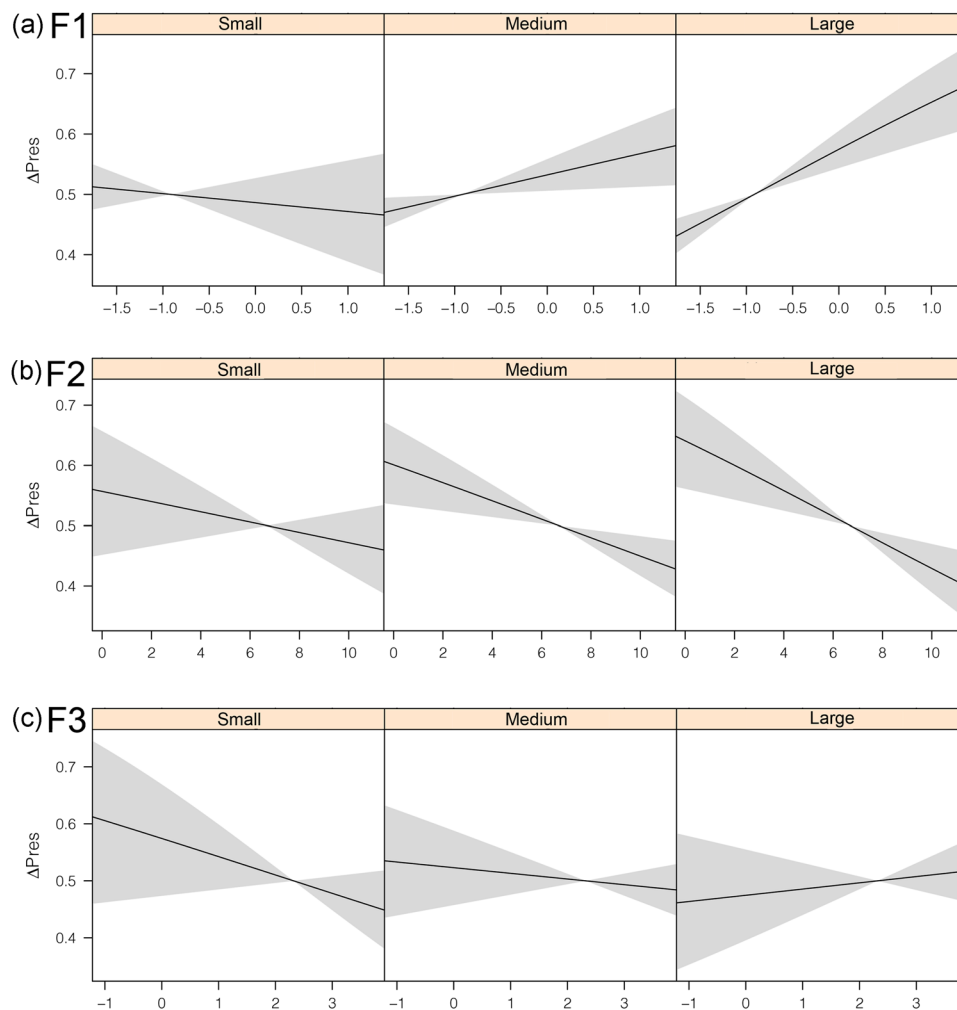
FIGURE 3 Partial responses of the three habitat variables on the probability of lemur species occurrence and their interaction with species average home range size. (a) F1: habitat area; (b) F2: fragmentation; and (c) F3: landscape complexity

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, Cuozzo, Jacky, & Lawler, 2012).

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

Fragmentation (F2) was more important than habitat availability (F1) and landscape complexity (F3) in determining the probability of presence of *Hapalemur* 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 (*Hapalemur griseus*) appear more sensitive to habitat area (F1), while species inhabiting relatively smaller or more fragmented areas (i.e., *Hapalemur aureus* and *Hapalemur 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, & Brenneman, 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 R eserve 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, & Chikli, 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, Rakotovao, 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 *Hapalemur* 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.

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SUPPORTING INFORMATION

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

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