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 (5 genera) and Indriidae (2 genera). We fitted Generalized Linear Models to determine the role of habitat fragmentation characteristics, e.g., forest cover, patch size, edge density, and landscape configuration, as well as the protected area 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 protected areas 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 significantly 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, species distribution, anthropogenic disturbance, Lemuridae, Indriidae, Madagascar

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" (Gibson et al., 2013; Dirzo et al., 2014; Galetti et al., 2017). 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; Gibson et al., 2011, 2013; Laurance et al., 2011; Dirzo et al., 2014; 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 (Dirzo et al., 2014; Ceballos, Ehrlich, & Dirzo, 2017).

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). Within Madagascar, which is considered to be a biodiversity hotspot due to its many endemic species listed as Endangered or Critically Endangered by the IUCN (Myers, Mittermeier, Mittermeier, Da

Fonseca, & Kent, 2000), ninety-four percent of the 113 currently described lemur species are threatened with extinction, making them 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 (Harper, Steininger, Tucker, Juhn, & Hawkins, 2007; Hannah et al., 2008; Ganzhorn, Lowry, Schatz, & Sommer, 2001; Ganzhorn, Wilmé, & Mercier, 2014; 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 meters (Vielledent 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 (Razafimanahaka et al., 2012; Golden, Bonds, Brashares, Rasolofoniaina, & Kremen, 2014). The hunting of lemurs is illegal, but consumption of bushmeat in Madagascar is widespread, with poor rural households often targeting large diurnal lemur species (Golden, 2009; Jenkins et al., 2011, Borgerson, McKean, Sutherland, & Godfrey, 2016). 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, e.g., *Lemur catta* (Gould & Sauther, 2016; LaFleur, Clarke, Reuter, & Schaefer, 2019).

Previous studies predicted that a majority of lemur species will experience massive range shifts, contracting the amount of habitat available to them (Brown and 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 (Ganzhorn & Eisenbeiß, 2001; Bodin & Norberg, 2007; Boyle & Smith, 2010; da Silva, Ribeiro, Hasui, da Costa, da Cunha, 2015; Schüßler, Radespiel, Ratsimbazafy, & Mantilla-Contreras, 2018; Steffens & Lehman, 2018), however, anthropogenic effects often occur at a landscape-level (Arroyo-Rodríguez et al., 2013; Arroyo-Rodríguez & Fahrig, 2014; Galán-Acedo et al., 2019a; Galán-Acedo, Arroyo-Rodríguez, Estrada, & Ramos-Fernández, 2019b). 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 (1) 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 (2), 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 modelled the role of various habitat characteristics on large-bodied diurnal/cathemeral species presence 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 (Lee, 2003; Wieczkowski, 2003; Isaac & Cowlishaw, 2004; Boyle & Smith, 2010; Nowak & Lee, 2013; Donati et al., 2016; Eppley et al., 2017). 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), we modelled the role of several 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 (Estrada & Coates-Estrada, 1996; Rode, Chapman, McDowell, & Stickler, 2006; Boyle & Smith, 2010; Donati et al., 2011; Campera et al., 2014). 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 (Plumptre & Reynolds 1994; Ganzhorn 1995; Chapman, Chapman, Bjorndal, & Onderdonk, 2002; Eppley, Donati, & Ganzhorn, 2016), though folivorous primates can be highly selective and potentially require equally large home ranges (Snaith & Chapman, 2005). Considering the large-bodied lemurs, we expect genera such as *Varecia* and most *Eulemur* to be severely affected by habitat availability and fragmentation due to their high reliance on fruit resources and need for larger home ranges. By comparison, generalist folivores, e.g., *Hapalemur*, *Prolemur*, *Indri* and some *Propithecus*, especially those with smaller home ranges, are expected to be the least affected. We expect that lemurs with folivore-frugivore diets (e.g., *Lemur catta*, some *Eulemur* and some *Propithecus*) will display intermediate effects due to fragmentation.

Methods

Data collection

We obtained occurrence points for all diurnal and cathemeral lemur species, totaling 32 taxa, from the dataset collated by Tinsman (2019). These include the genera *Eulemur* (12 species), *Lemur catta*, *Hapalemur* (4 species), *Prolemur simus*, and *Varecia* (2 species / 3 subspecies) from the family Lemuridae, and *Propithecus* (9 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 area immediate area surrounding Lac Alaotra (Rendigs et al., 2015), thus we did not have enough distribution points to allow for comprehensive modelling. Three types of sources were utilized: 1) points collected in the field by co-authors, 2) online databases including the Global Biodiversity Information Facility (GBIF), Mammal Networked Information System (MaNIS), VertNet, Madagascar Lemurs Portal, and Reseau de la Biodiversité de Madagascar (ReBioMa), and 3) 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 dataset. Further, we only retained 1 occurrence point per 1-km cell. We were left with a remainder of 3,006 reliable and unique occurrence points (Figure S1).

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 done in Vielledent et al., 2018. Most of our occurrence data come from protected areas which are expected to be, on average, less fragmented and degraded; therefore in order to avoid potential biases due to more frequent sampling in protected areas, we also downloaded a spatial layer of the Madagascar Protected Area Network, hereafter referred to as Protected Areas (PA), from the online database Reseau de la Biodiversité de Madagascar (ReBioMa) (Fig. S2). Nearly all forests in Madagascar exhibit some relative degree of fragmentation (Vielledent et al., 2018), thus PAs include both fragmented and less fragmented forests.

Data preparation and fragmentation analysis

We used the binary forest maps (0 = non-forest; 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 3 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), i.e., measuring the physical shape of the habitat (Table 1; Table 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 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 (Fleming, Breitwisch, & Whitesides, 1987; Donati et al., 2017), 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. / *Prolemur simus*, some *Propithecus* spp., and *Indri indri*), seven species are folivore-frugivores (some *Eulemur* spp., some *Propithecus* spp., and *Lemur 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).

Modelling

We tested for the effect of fragmentation on the species probability of presence using a species distribution modelling 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. Thuiller, Lafourcade, Engler, & Araújo, 2009; Brown & Yoder, 2015). 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 non-forested 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 protected area variables as predictors (Table 1). Including protected areas separately from the fragmentation axes allowed us to estimate the relative contribution of fragmentation to the relative probability of presence of species while controlling for the confounding effect of protected areas. 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 both the full models and the selected models.

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 protected areas) 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, $P = 0.103$). We present both the full models and the selected models, and in the latter case we opted for selecting the best fit model with the lowest number of parameters (Arnold et al., 2010).

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” (Hijman & 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.

Results

In general, all habitat variables tested were important for most of the species (Figure 1; Table S4), though five species, i.e., *E. mongoz*, *E. macaco*, *P. deckenii*, *P. coronatus*, and *P. 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 modelled). This F1 component had a positive effect on the distribution of these ten species, mostly *Eulemur* and *Propithecus*. The second component (F2) accounting for habitat fragmentation was significant in 14 taxa (43.8% of lemurs modelled), always showing a negative effect, therefore indicating that for most species the probability of presence is lower when the habitat is fragmented. These 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 modelled), negatively affecting the distribution of *H. occidentalis* and *V. v. subcincta* (Figure 1; Table S4). Protected areas showed a positive effect in 37.5% of taxa modelled (Figure 1; 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 consistent negative effect of fragmentation (see Figure S3; Table S5 for full model results).

Using the data from the selected models, the effect of traits on the fragmentation metrics was limited. Habitat area (F1) had a positive effect on lemur species and a positive interaction with home range area, suggesting that habitat area is especially important for species with large home ranges (Figure 2; Tables S5, S6). For fragmentation (F2), there was negative effect for all species, regardless of home range size (Figure 3; Tables S5, S6).

Considering the full model for the trait-specific analysis, the effect of 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 4a; Table S7). Regarding F2, all dietary guilds, i.e., folivores, frugivores, and folivore-frugivores, were negatively affected by patch and edge density (Figure 4b; Table S7). The negative effect of F2 became more strongly negative with increased home ranges of lemur species (Figure 5b; Table S7). Landscape complexity (F3) negatively affected both folivores and frugivores, while having a strongly positive affect on folivore-frugivores (Figure 4c; Table S7). Finally, landscape complexity negatively affected species of both small and medium home range sizes, though positively affected species with large home range sizes (Figure 5c; Table S7).

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). Lastly, landscape complexity does not appear to play a large role effecting 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).

True lemurs: Eulemur *spp.*

Our analyses seem to mirror previously reported effects on the diverse *Eulemur* clade (Bayart & Simmen, 2005; Schwitzer, Randriatahina, Kaumanns, Hoffmeister, & Schwitzer, 2007; Donati et al., 2011; Brenneman et al., 2012; Tecot, 2013; Balestri et al., 2014; Campera et al., 2014), 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 *E. albifrons*, *E. fulvus*, and *E. rubriventer*. All three have large species ranges, though *E. 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 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 (*E. macaco*) nor mongoose lemurs (*E. mongoz*) showed any effects to protected areas 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 multi-male multi-female social groups), and as such, many species within are considered ecologically flexible primates (Overdorff, 1993a, 1993b; Donati, Bollen, Borgognini-Tarli, & Ganzhorn, 2007; Donati et al., 2011, 2016; Ossi & Kamilar 2006; Kappeler & Fichtel, 2016; Sato et al., 2016). Western species that occur within the seasonal, deciduous forest seem to be more vulnerable to fragmentation and edge area (Kamilar & Tecot, 2016; Sato et al., 2016). Smaller home-range requirements in western species compared to eastern species (Overdorff, 1993a; Curtis & Zaramody, 1998; Donati, Lunardini, & Kappeler, 1999; Schwitzer et al., 2007; Donati et al., 2011; Sato et al., 2016) 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 and the 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 theshold of habitat pulverization 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 (Tecot, 2013; Balestri et al., 2014).

Ring-tailed lemurs: Lemur catta

Similar to some of the dry forest brown lemurs, our analysis revealed that ring-tailed lemurs (*L. catta*) was significantly affected by fragmentation and protected areas. 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 (Sauther, Sussman, & Gould, 1999; Goodman, Rakotoarisoa, & Wilmé, 2006; Gould, 2006; Jolly, Koyama, & Rasamimanana, 2006; LaFleur & Gould, 2009;

Axel & Maurer, 2011; Kelley, 2011; Cameron & Gould, 2013; Donati et al., 2013; Gabriel, 2013). They are also semiterrestrial and known to exploit anthropogenic landscapes (Sauther et al., 2006; LaFleur & Gould, 2009; Gabriel 2013), yet it is suggested that this species is sensitive to moderate habitat disturbance as populations occurring in poor quality habitats have lower densities (Sussman, Green, Porton, Andrianasolondraibe, & Ratsirarson, 2003; Kelley, 2011; Gabriel, 2013). Thus, their flexibility in being able to exploit areas outside of strict forest habitat at least may allow this species to sustain populations within fragmented landscapes (Anderson, Rowcliffe, & Cowlishaw, 2007; Gabriel, 2013). Contrary to many recent publications (Sussman et al., 2003; Axel & Maurer, 2011; Cameron & Gould, 2013), however, our findings show that similar to most lemur species, PAs represent a widespread positive effect on the distribution of *L. catta*. Either way, 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).

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 / *Prolemur simus*. Bamboo lemurs are folivorous, and their ecological flexibility may allow bamboo lemurs to persist in heavily altered environments, allowing them utilize edge habitat (Grassi, 2006; Eppley et al., 2015, 2016, 2017). Not all bamboo lemurs, however, are able to cope with habitat fragmentation. 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 (Wright et al., 2008; Ravaloharimanitra et al., 2011). 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). Contrary to other genera, PAs were not an important predictor of *Hapalemur* spp. presence. Furthermore, PAs did not show a positive effect on the distribution of the greater bamboo lemur (*P. simus*), and this may be due to it only being known from a small number of recently discovered sites (Wright et al., 2008; Ravaloharimanitra et al., 2011). 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).

Ruffed lemurs: Varecia rubra *and* Varecia variegata *ssp.*

The various habitat metrics provided similar results across ruffed lemur taxa. Habitat area (F1) had a positive effect on *Varecia 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 (Rigamonti, 1993; Vasey, 2000; Ratsimbazafy, 2006), 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 (White, Overdorff, Balko, & Wright, 1995; Balko & Underwood, 2005; Herrera, Wright, Lauterbur, Ratavonjanahary, & Taylor, 2011). Though generally true, *V. v. editorum* is known to inhabit less than ideal habitat, e.g., shifting cultivation and secondary forest (Hekkala, Rakotondratsima, & Vasey, 2007), forest restoration zones (Martinez & Razafindratsima, 2014; de Winter et al., 2018), and even in degraded fragments intermixed with coffee plantations (Holmes et al., 2013), thus providing an explanation as to why this taxon 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 (Vasey, 2004; Louis et al., 2005; Holmes et al., 2013; Baden et al., 2014), 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. variegata 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 (Louis et al., 2005; Dunham, Erhart, & Wright, 2010).

Sifaka and indri: Propithecus *spp. /* 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 *Indri indri*. Sifaka (*Propithecus* spp.) are relatively widespread throughout most Madagascar habitats, i.e., eastern humid, dry/humid deciduous, and spiny desert (Mittermeier et al., 2010). For example, fragmentation had a strongly negative effect on the distribution of golden-crowned sifaka (*P. tattersalli*), a species endemic to the Daraina region of northern Madagascar. According to Quéméré, Amelot, Pierson, Crouau-Roy, & Chikhi (2012), however, the small remaining population of golden-crowned sifaka had contracted prior to human arrival. Interestingly, the distribution of Perrier's sifaka (*P. perrieri*) a little further north 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 *P. coquereli* and *P. candidus*. The main difference is that the former inhabits an extremely fragmented western deciduous forest, while the latter is found in a few large, humid eastern forest blocks (Pichon et al., 2010; Salmona et al., 2014). Despite these habitat differences, all *Propithecus* spp. are threatened by habitat loss from charcoal production and shifting cultivation (Schwitzer et al. 2013; Kun-Rodrigues et al., 2014).

Considering all nine sifaka species, both *P. diadema* and *P. verreauxi* inhabit the largest geographic areas, the central-northeastern humid forest and the dry deciduous / spiny desert of the southwest, respectively (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 which inhabit distinctly different biomes, and is likely due to *P. verreauxi* inhabiting more seasonal and heavily fragmented forests in western and southwestern Madagascar (Axel & Maurer, 2011). 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 (Mittermeier et al., 2010; Junge, Barrett, & Yoder, 2011). 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 affect of PA on indri presence.

Trait-specific sensitivity to fragmentation

Overall, lemurs' functional traits appear to be affected by habitat availability, fragmentation and configuration as expected. Our results showed that species with larger home range were more positively affected by habitat availability (Figure 2), indicating that species with small home range areas are more tolerant to habitat loss than species with large home range areas. We also detected a negative effect of fragmentation across species, but no interaction with home range size (Figure 3). These results are mirrored our full model trait-specific models (Figure 5).

Our full 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 in order 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, e.g., *E. rufus*, *L. catta*, and *P. tattersalli* among others, to disproportionately inhabit smaller habitat patches and/or more open forests. It is important to note that the diet of *Propithecus* is diverse and species are classified as either folivores or folivore-frugivores

(Hemingway, 1998; Powzyk & Mowry, 2003; Norscia, Carrai, & Borgognini-Tarli, 2006; Irwin, 2008; Sato et al. 2016; Koch, Ganzhorn, Rothman, Chapman, & Fichtel, 2017), thus the folivore models may be more strongly influenced by other ecologically-specialized lemurs, e.g., 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 (Ganzhorn, 1995; Lehman, Rajaonson, & Day, 2006; Eppley et al., 2015, 2017), while frugivorous lemurs have been shown to be adversely affected by anthropogenic, degraded habitat (White et al., 1995; Balko & Underwood, 2005; Herrera et al., 2011). As frugivorous lemurs are important seed dispersers, they are essential for the maintenance of forest diversity and play a fundamental role in habitat regeneration (Ganzhorn, Fietz, Rakotovao, Schwab, & Zinner, 1999; Wright et al., 2011; Razafindratsima & Dunham, 2014; Federman et al., 2016). 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 (Lehman et al., 2006; Sato et al., 2016; de Winter et al., 2018). 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

Potential caveats

In this study we made a number of assumptions in order to estimate the effect of habitat availability, fragmentation and complexity on the probability of species' presence. First, in order 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 (Chapman, Lawes, Naughton-Treves, & Gillespie, 2003; Araújo & Guisan, 2006). 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, Figure S3). Fourth, it is possible that the positive effect of PAs is a genuine effect suggesting that species in 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 protected areas. 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.

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 (Hannah et al., 2008; Kremen et al. 2008; Irwin et al. 2010; Campera et al. 2014; Eppley et al. 2015, 2017), 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 (Wrangham & Ross, 2008; Wright et al., 2012; Campera et al., 2017). As PAs were shown to be the best 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 (Barrett, Brown, Morikawa, Labat, Yoder, 2010; Allnutt, Asner, Golden, & Powell, 2013). Even just considering Madagascar forests in general, the mean distance to edge has been estimated at 300m, 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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Table

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 protected areas)	Protected Area network (1 = inside protected area; 0 = outside protected area)

Figure legends

Figure 1. Heatmap showing the directional influence of various habitat metrics (F1: habitat area; F2: fragmentation; F3: landscape complexity) and protected area (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.

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

Figure 3. Partial response 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; c) F3: landscape complexity.