



# Prioritizing protected areas in Madagascar for lemur diversity using a multidimensional perspective

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## ABSTRACT

Biodiversity is affected by anthropogenic activities, with a trend of decreasing species richness with habitat degradation. Decreasing species richness erodes evolutionary history and ecosystem function, but taxonomic, phylogenetic and functional diversity can have contrasting patterns. It is essential to measure these dimensions of biodiversity explicitly and assess how they are valued in prioritizing protected areas (PAs) to conserve diversity. Madagascar is a biodiversity hotspot, with high diversity and endemism coupled with heavy anthropogenic pressure. The endemic primates – lemurs – are the most endangered mammal taxon. A recent action plan prioritized PAs based on lemur species richness, weighted by endangerment. This scheme does not capture the evolutionary, functional, or biogeographic components of biodiversity, nor does it directly assess the level of human threat to those PAs. I compiled the largest dataset on lemur community composition in 100 PAs, including almost all lemur species (98 species). I combined data on lemur occurrence, their phylogeny, functional traits, IUCN Red List status, and environmental variables including deforestation between the years 2000 and 2014. I ranked PAs based on 14 metrics as well as the sum of metrics to determine how PA priorities compare under different valuation schemes. Based on the sum of seven metrics, I identified the top 25 PAs for lemur conservation. With these priority rankings, I propose areas of high lemur diversity, habitat heterogeneity and productivity, and deforestation be the focus of future conservation activities to maximize community resilience and prevent the erosion of evolutionary diversity and ecosystem function.

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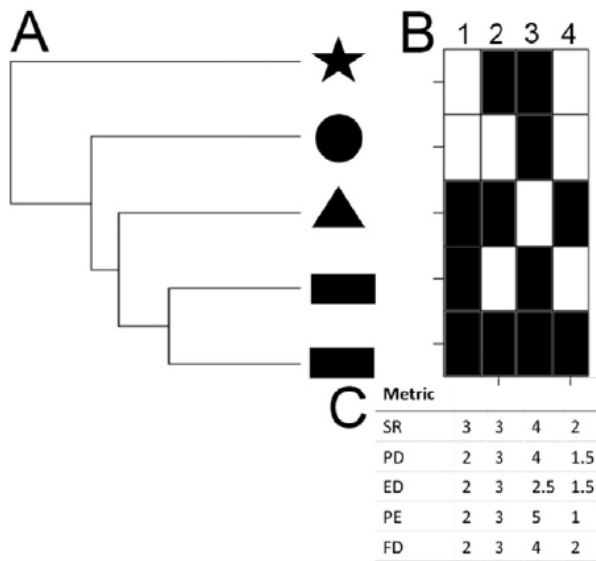
## 1. Introduction

Variation in the distribution of endangered, geographically restricted, functionally and evolutionarily distinct species has made the prioritization of conservation areas difficult (Karp et al., 2015). By what measure should conservation biologists and policy makers quantify and rank areas to compare them and choose which deserve protection and funding? Are there habitat features that promote exceptional biodiversity, such as heterogeneous or highly productive habitats, and if so can these habitat variables be used as proxies for biodiversity to rank areas? The sum of multiple dimensions of biodiversity and habitat productivity, weighted by the threat of species extinction and rate of local habitat loss, provides a multidisciplinary measure of biodiversity and endangerment to rank conservation areas.

Species richness has been quantified for many areas around the globe, and there is a general trend for decreasing species richness with human disturbance (e.g., Newbold et al., 2015). Species richness has long been used as a measure of biodiversity and proxy for ecosystem function, but it does not capture the evolutionary history represented

by species, nor does it always reflect the influence of evolutionary history and trait diversity on community function, stability and resilience. The functional and evolutionary distinctiveness of species and communities provides unique, historical depth to measures of biodiversity, as well as direct ties to ecosystem function and services provided for people (Naeem et al., 2016; Purvis and Hector, 2000). For example, conservation practitioners may opt to weigh species' presence by their phylogenetic diversity and distinctiveness, which directly measure the evolutionary history represented by a community or individual species (Faith, 1992; Faith et al., 2004; Graham and Fine, 2008; Isaac et al., 2007). In two communities with the same species richness, one community may encompass more of the phylogeny than another (Fig. 1). Preserving evolutionary history may warrant higher priority than species richness alone when some species represent the irreplaceable heritage of a lineage (Faith, 1992). Similarly, phylogenetic endemism reflects the geographic isolation of evolutionary history, identifying areas that may be relicts of deep-time biodiversity found nowhere else (Rosauer et al., 2009) (Fig. 1). Such areas may be higher priority for conservation because of the ancient geographically restricted biodiversity they harbor. Species and phylogenetic complementarity capture variation in the uniqueness of species and the phylogenetic history represented if certain species are preserved (Jensen et al., 2016), and

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**Fig. 1.** Schematic illustrating how community diversity varies depending on the metric used to quantify diversity. A) Phylogeny of species with shapes representing functional traits of species. B) Diagram illustrating the presence (black) and absence (white) of each species (rows) in each of four sites (columns, labelled 1–4). C) Diversity metrics for each site, illustrating how sites with the same species richness (sites 1 and 2) can have different phylogenetic and functional diversities. SR: species richness, PD: phylogenetic diversity, ED: evolutionary distinctiveness, PE: phylogenetic endemism, FD: functional diversity.

complementarity of communities quantifies the degree to which protected areas represent unique biomes (Faith et al., 2004). Functional diversity directly measures the traits of species that make up communities (Fig. 1), especially ecologically relevant traits related to how species partition niches (Zuppinge-Dingley et al., 2014), how productive communities are (Gamfeldt et al., 2013), and how resilient they are to changes in the environment (Oliver et al., 2015). Taxonomic, phylogenetic and functional diversity are frequently assumed and/or found to be positively related, but they are not always, making it imperative to have functional trait data to complement taxonomic and phylogenetic information (Devictor et al., 2010).

The diversity of communities on its own does not reflect the level of anthropogenic threat to those communities. One scheme for assessing the value of an area that integrates anthropogenic threats is to weight the presence of species by their endangerment status; e.g., by their IUCN Red List status (Schwitzer et al., 2014). Similarly, the evolutionary distinctiveness of species, as measured by the amount of unique evolutionary history represented by a species, can be weighted by the Red List status, yielding the evolutionarily distinct and globally endangered index, EDGE (Isaac et al., 2007). Incorporating the phylogenetic complementarity of species with their probability of extinction yields the I-HEDGE index (Jensen et al., 2016). These schemes allow the community composition to be weighted by the threat level to individual species, but the level of threat to particular areas should also be a factor in conservation priority zonation. For example, data on land cover over time in areas may be used to assess the rate of habitat loss and quantify anthropogenic threat, and these data are available at global scales (e.g., Hansen et al., 2013). While the IUCN Red List status takes habitat loss (measured or estimated) into account, it is also weighted heavily by the projected population change (measured or estimated), hunting pressure, and harvesting for trade. Where new habitat loss data have not been incorporated into the IUCN status, including the latest estimates of deforestation is important to re-evaluate the threat status of species and communities. Therefore, I argue that in prioritizing conservation efforts, the diversity of the area as well as the anthropogenic threats should be taken into account.

Madagascar is a biodiversity hotspot (Myers et al., 2000), with rapid loss of hundreds of threatened, endemic species (Allnutt et al., 2008;

Goodman and Jungers, 2014) and a high rate of habitat loss due to slash-and-burn agriculture, clearing land for pasture and commercial mining (Harper et al., 2007; Scales, 2014), as well as heavy hunting pressure in some regions (Borgerson, 2015; Borgerson et al., 2016; Golden, 2009). The primates of Madagascar – the endemic lemurs – are the most endangered mammal taxon, with ~95% considered threatened with extinction (Schwitzer et al., 2014). Recent efforts to prioritize protected areas (PAs) for lemur conservation have weighted the species richness of PAs by the IUCN Red List categories of those species, and set conservation initiatives for the top-ranking PAs (Schwitzer et al., 2014). The Lemur Action Plan specified activities to be conducted in the top-ranking PAs between the years 2013 and 2016 to stave off further lemur extirpations (Schwitzer et al., 2013). The PAs were not evaluated for their ranks in other measures of diversity, however, potentially prioritizing sites that would not have high rank based on other dimensions of biodiversity.

Measuring diversity at the species level does not capture the evolutionary histories of species and contrasts with others who have advocated assessing conservation priorities based on the phylogenetic distinctiveness of species as a measure of the evolutionary history represented by each species (Isaac et al., 2007; Lehman, 2006; Purvis and Hector, 2000). Hotspots of evolutionarily distinct lemur species, phylogenetic diversity and endemism, and taxonomic richness do not align perfectly, each suggesting different priority areas (Gudde and Venditti, 2016; Gudde et al., 2013; Lehman, 2006). Previous studies on phylogenetic diversity of lemurs have used incomplete and poorly resolved phylogenies, and no previous study has quantified functional trait diversity. Importantly for this study, previous evaluations of phylogenetic diversity have not quantified diversity at the level of PAs, but rather at coarse resolutions of regions or grid-cells, the latter without ground-truthed verification of species occurrences. PAs should be the unit of analysis given that these are the designated localities of conservation action, and rather than seek out new areas, this paper aims to evaluate the conservation priorities of existing PAs. Finally, previous priority rankings have not taken into account environmental factors such as habitat heterogeneity, plant productivity, or the amount of habitat loss. I argue that priority rankings based solely on species richness weighted by species' threat statuses fail to capture diversity in multiple dimensions and should be reconsidered. This paper evaluates PAs in a new light with comprehensive data that have not been combined until now, including almost all lemurs, their phylogenetic relationships, functional traits, extinction risk, and the quality of the environment.

Here, I examined 100 PAs, quantifying lemur diversity in terms of species richness and complementarity, phylogenetic diversity and endemism, evolutionary distinctiveness and complementarity of species, and functional trait diversity, with and without weighting by species endangerment. I measured elevational heterogeneity and plant productivity from remotely-sensed data, which have been shown to be significant predictors of diversity (Jetz and Fine, 2012), and the amount of recent forest loss. I compared the ranks of PAs from each of my metrics as well as a combined metric to previous priority rankings (Schwitzer et al., 2013), and found differences that suggest previous rankings under-represented threatened biodiversity. I rank the top 25 PAs and find that PAs in the northeastern rainforests and northwestern mosaic dry forests are the highest priorities, while PAs in the southwest ranked lower based on lemur diversity, but highest based on deforestation. This new ranking system provides a more comprehensive assessment of the lemur and habitat diversity as well as threat status of Madagascar PAs than previous efforts, although I suggest socio-cultural and economic data are also needed to measure the value of PAs for people.

## 2. Methods

I first assembled a database of Madagascar bioregions and protected areas (PAs), lemur geographic ranges, and environmental variables. I then quantified taxonomic, phylogenetic and functional alpha diversity

and phylogenetic endemism within PAs. I calculated the area and percent forest cover in PAs in the year 2000 and the loss of forest until 2014 (Hansen et al., 2013) to estimate the total area and percent forest loss within protected areas.

### 2.1. Study sites

I defined five biogeographic regions based on the delineation of ecoregions subdivided by river barriers (Ganzhorn et al., 2006) and georeferenced them in a geographic information systems (GIS) database (Supplementary data deposited online, Appendix A). All layers used the WGS 84 coordinate system unless otherwise noted. These bio-regions contain unique habitat types and have been suggested to be related to species endemism because of river/habitat barriers among them (Ganzhorn et al., 2006).

Protected areas (PAs) are useful community-level units for analysis because they are tracts of forest with boundaries set aside for conservation purposes and have been inventoried for lemurs. I obtained polygon shapefiles of over 100 PAs around Madagascar from the nongovernment organization CIRAD (Desbureaux et al., 2016, SAPM ver. 20101205, Appendix A Dataset 5). I included terrestrial PAs with more than two species of lemurs present. This includes PAs that were established before 2003 and considered national parks, protected by the Madagascar National Parks (AP gérée par MNP,  $n = 42$ ), extensions of national parks ( $n = 2$ ), new protected areas (Nouvelle Aire Protégée,  $n = 39$ ), PAs considered temporary (Aire Protégée à Statut Temporaire,  $n = 16$ ), and one private reserve (Berenty). The exact boundaries of some PAs, especially the new PAs, have been contentious, but the shapefile used in this study represents the state of the PAs in 2014. The shapefile used here closely matched that available from REBIOMA in 2013 (<http://atlas.rebioma.net/>). To generate species presence/absence matrices at regional and local scales, I obtained polygon shapefiles of extant lemur range maps from the IUCN terrestrial mammal database (<http://www.iucnredlist.org/technical-documents/spatial-data>, accessed 2/18/2015). I verified each lemur range against primary and secondary sources to verify the limits of species distributions, editing polygons where necessary (Appendix A). I tabulated a community presence/absence matrix (species X protected area) using the *intersect* function in the package *raster* (Hijmans, 2015) for the R statistical environment (R Core Team, 2014). Presence/absence matrices were then verified against literature sources of ground-truthed surveys at the PAs and reports from field experts (Appendix A). A literature search was conducted using Google Scholar with the keywords: 'lemur', 'inventory', 'survey', and the names of the protected areas (conducted between 1/16/2016 and 1/26/2016). Forty four papers, reports, and datasets were found, with publication dates between 1997 and 2016, and lemur surveys conducted between 1975 and 2015, with 66% of studies conducted between 2000 and 2015. This literature review was a thorough evaluation of the available information on lemur distributions and represents our best knowledge to date. The information used requires updating, however, and a revision with recent surveys and unpublished data from field experts would improve the resolution of the findings presented here.

### 2.2. Study species

I used a total evidence phylogeny that included ~90% of living lemurs (Herrera and Dávalos, 2016, Appendix A). Species that were missing from the original phylogeny (16 species) did not have comparable genetic loci to those used in the phylogenetic inference. Previous studies of lemur biogeography have included a subsampled diversity (e.g., ~36% of lemurs in Gudde and Venditti, 2016), but comparative biological inferences are affected by missing data. To include almost all lemurs, I grafted missing species onto the phylogeny manually based on the position of missing species to their congeners in the original publications (Appendix A). This resulted in the most complete dataset ever used

for lemur biogeography. The state of lemur taxonomy is in flux, and the number of species recognized has risen from ~50 recognized by some scholars in 2006 (Ganzhorn et al., 2006) to over 100 recognized in the most recent compilation (Mittermeier et al., 2010), with several new species described since then. Some of the newly erected taxa were formerly recognized as subspecies, while others are 'cryptic' species that were formerly recognized as one species. These taxonomic revisions have been met with skepticism (Markolf et al., 2011; Tattersall, 2007), but where rigorous tests have been done, the new species have been supported based on genetic, phenotypic, and geographic data (Markolf et al., 2013; Radespiel et al., 2011; Yoder et al., 2016; Yoder et al., 2005). Further, some newly erected species were later subsumed based on multidimensional data (Groeneveld et al., 2009). The taxonomy is still in flux, however, and to standardize, in this paper the taxonomy of Mittermeier et al. (2010) is used, with the addition of *M. gerpi* (Radespiel et al., 2011), *M. tanosi*, and *M. marohita* (Rasoloarison et al., 2013).

Variation in traits related to body size, diet and activity pattern in sympatric lemur species are important factors in niche partitioning that may be related to community composition (Ganzhorn, 1997; Ganzhorn, 1988; Kamilar and Ledogar, 2011). Data were compiled from the literature on the following variables: 1) body size (grams, natural log transformed), 2) diet category (folivore, frugivore, omnivore), and 3) activity pattern (diurnal, nocturnal, cathemeral, Appendix A Table S1).

### 2.3. Environmental and forest loss data

To quantify the environmental factors predicted to affect lemur community composition, I extracted elevation data for each PA from the WorldClim raster data layers and calculated the standard deviation of elevation with each PA as a measure of topographic heterogeneity (30 arc-second resolution, Hijmans et al., 2005). To quantify resource availability in terms of habitat productivity, I included the Net Primary Productivity (NPP) generated from the MODIS imagery of the NASA Terra satellite (<http://www.ntsg.umt.edu/project/mod17>, accessed 1/11/2016). I used the *extract* function in *raster* to calculate an unweighted mean of NPP. Forest cover and forest loss data were obtained from the high-resolution data products of Hansen et al. (2013), converted to UTM projection for area calculation, and I calculated the total and percentage of pixels with ~50% canopy cover, as well as the number of pixels with forest loss to calculate the total and percentage of forest loss in each PA. All the data for each PA are available online (Appendix A).

### 2.4. Diversity metrics

To compare the priority ranking of PAs based on the composition of local communities, I quantified taxonomic, phylogenetic and functional trait community alpha diversity at each PA, with the species lists for each region as the source pools. I also quantified phylogenetic endemism, with all lemurs as the source pool, using code from Rosauer et al. (2009) (<https://github.com/DanRosauer/phylospatial>, accessed 5/24/2016). For each PA, I calculated taxonomic diversity as the species richness, or total number of species with ranges overlapping the PA. I calculated the threatened species index by multiplying each species' presence by a quantitative scale of their IUCN threat status (Least Concern = 1, Near Threatened = 2, Vulnerable = 3, Endangered = 4, Critically Endangered = 5, accessed 2/18/2015). The conservation status of all lemurs was re-evaluated in 2012, and ~38% of species that were formerly data deficient were raised to near threatened or threatened status. For most species, their endangered status was based on observed or predicted declining population size due to high habitat loss across the island, with many species hunted for bushmeat (Borgerson et al., 2016; Golden, 2009), and at least 17 lemur species exploited for the illegal pet trade, especially *Lemur catta* (Reuter et al., 2016). The updated lemur conservation status represents our current understanding,

although updates are needed with new information on species distributions, population size estimates, and local threats. I calculated phylogenetic community structure using the mean nearest taxon index (MNTD), which is a measure of the mean pairwise branch-length distance among pairs of co-occurring taxa (Webb, 2000). I assessed if MNTD differed significantly from expectation based on species richness by comparing the observed MNTD value to that expected given a null distribution from randomizing the presence/absence matrix but maintaining species prevalence (richness null model, in *picante* Kembel et al., 2010). Negative MNTD values with a probability of meeting the null expectation  $< 0.05$  were considered phylogenetically clustered – species are more closely related than expected by chance – while positive MNTD values with probabilities  $> 0.95$  were considered phylogenetically overdispersed – species are more distantly related than expected. The reason for using MNTD instead of, for example, phylogenetic diversity *sensu* (Faith, 1992) is that MNTD measures the dispersion of species across the tree such that we may choose to prioritize a PA with species that come from distant parts of the phylogeny (akin to local phylogenetic complementarity) rather than a PA that has several closely related species that represent a less diverse phylogenetic history. Further, ED (explained below) measures the phylogenetic diversity of each species in a way related to phylogenetic diversity *sensu* Faith (1992), and I chose to avoid double-counting the total phylogenetic history represented by a species. Functional trait diversity was quantified using MNTD, calculated based on the Gower dissimilarity matrix from the trait dataset (Maechler et al., 2015). The evolutionary distinctiveness of each species in the communities (ED) was quantified using summed unique branch-lengths represented by species (Isaac et al., 2007), as calculated in *caper* (*ed.calc* function, Orme, 2013). ED was weighted by the natural log of the conservation status, yielding the evolutionarily distinct and globally endangered (EDGE) metric, as in its original description (Isaac et al., 2007). Recent revisions to the EDGE paradigm evaluate the complementarity of species in terms of phylogenetic history preserved if the highest priority species is ‘saved’, and species are ranked based on the phylogenetic history they would preserve if they are conserved (HEDGE Jensen et al., 2016). Phylogenetic endemism was calculated, taking into account the geographic restriction of phylogenetic branch-lengths to PAs (Rosauer et al., 2009). The species and phylogenetic complementarity of each PA was quantified using beta diversity metrics, which measure the dissimilarity of the species and phylogenetic branches in communities; the higher the average beta diversity, of a site, the more dissimilar it is from any other PA and thus provides high complementarity. Specifically, I quantified dissimilarity using the Sorenson and phylogenetic Sorenson indices (using *vegan*, Oksanen et al., 2013, and *picante* packages, respectively, in R). Each PA was ranked based on the values of each metric, such that the PAs with the highest values were given a rank of 1. These measures were correlated (Table S2), suggesting they are each measuring overlapping aspects of community structure. Therefore, in addition to ranking PAs based on each of these metrics, I also summed ranks based 1) diversity metrics that minimized collinearity: the sum of species’ HEDGE ranks in each PA, phylogenetic and functional diversity, and the mean Sorenson’s index, 2) metrics of habitat: NPP, standard deviation of elevation, and percent forest loss, 3) the diversity and habitat metrics. I chose to give the overall rank of each PA as the sum of diversity and habitat metrics because those metrics provide the most comprehensive summary of diversity, threat, and habitat suitability (Appendix A).

### 2.5. Analyses

I tested the relationships among lemur diversity metrics using linear mixed models, in which each metric was z-score transformed, and a correlation structure was included based on the latitude and longitude of each PA centroid to account for spatial autocorrelation, as well as grouping PAs based on the region within which they occur to further accommodate non-independence due to sharing the same biogeographic

region (*lme* function in the R package *nlme*, Pinheiro et al., 2011). The ranks of each PA based on the threatened species index of Schwitzer et al. (2013) were compared to the ranks based on all the other measures using Wilcoxon paired rank tests in R. Significant deviation from 0 rank differences indicates that ranks based on different measures are not equivalent. The correlations among ranks for each metric, the summed ranks, and ranks based on habitat characteristics related to productivity (NPP) and topographic heterogeneity (standard deviation in elevation) were tested using Spearman’s rank correlations.

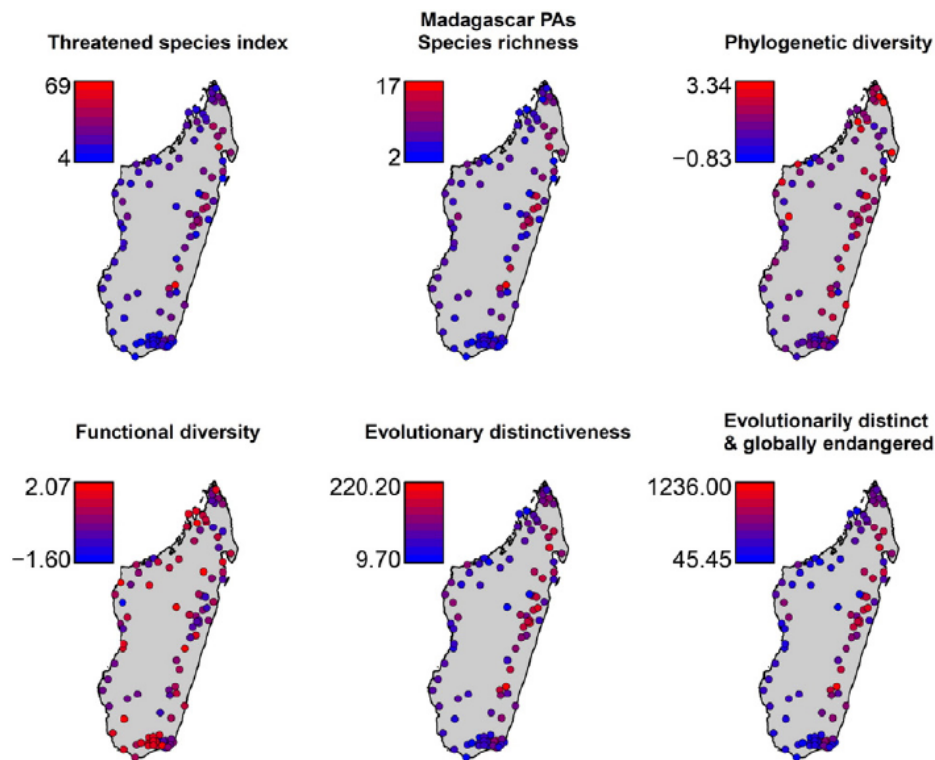
Diversity was mapped to visualize the distribution of diversity based on different measures. I reported the top 25 most diverse and threatened PAs for all of Madagascar, as well as provided the complete ranking in Appendix A. Based on the lemur diversity and threat level, I recommend the top 25 PAs be emphasized in further prioritization of conservation areas in Madagascar. I recognize that PAs should also be ranked based on measures that quantify different valuation schemes; for example, other taxonomic groups, as well as the impact of PAs for people. Future studies should focus on the socio-cultural and economic values of PAs to local populations and at the country level to prioritize PAs as well.

## 3. Results

Diversity, endemism, habitat variability and productivity, forest cover and forest loss were not perfectly matched across the landscape (Fig. 2). While most variables were positively correlated, functional diversity was negatively and least strongly related to other diversity metrics (Table 1). Functional diversity decreased with increasing percentage of forest cover ( $r = 0.18, p = 0.12$ ) and increased with increasing forest loss ( $r = 0.09, p = 0.19$ ), although these correlations are weak and not statistically significant. This result indicates that greater species richness does not increase functional diversity, which may be due to species having similar functional traits in species rich PAs. Maximizing ecosystem function is recognized as crucial to preserving ecosystem services, and functional redundancy increases resilience in communities because if some species go extinct locally, there are other functionally similar species to replace them and maintain functionality. The positive correlation between functional diversity and forest loss reveals that the PAs with the most functionally diverse and species poor lemur communities have the greatest anthropogenic threat. These correlations should be interpreted with caution, however, because they were not statistically significant.

The deforestation in PAs between the years 2000 and 2014 based on remotely-sensed forest cover totaled  $\sim 3000$  km<sup>2</sup>, with the highest deforestation occurring in montane rainforest PAs, such as Mangabe and Maromizaha. Western and southwestern PAs have also had high habitat loss, including Ranobe and the Kalabenono complex (SI Dataset 2). Such high deforestation rates within PAs illustrates the need for targeted conservation efforts to reduce the threats to natural habitats.

The rankings of PAs based on the threatened species index differed significantly from ranks based on all other measures (Wilcoxon signed ranks test,  $p < 0.001$  for all comparisons, Table S3). PAs ranked as high priority based on phylogenetic diversity and endemism as well as functional diversity were low priority based on the threatened species richness (Table 2). Rankings of PAs based on habitat characteristics found to promote lemur diversity (NPP and/or standard deviation of elevation) were positively correlated with rankings based on PA diversity measures, suggesting that PA selection and prioritization may be done with habitat features alone (Spearman correlations,  $p < 0.001$  for all comparisons, Table S2). This is especially useful when accurate data on lemur diversity are lacking; even in the absence of data on lemur community composition, it is possible to extrapolate from these results and judge if an area may harbor high diversity based on its remotely-sensed productivity and topographic heterogeneity.



**Fig. 2.** Spatial distribution of protected areas (PAs) colored by their values for lemur diversity, forest cover and deforestation, in which PAs labelled in blue are low conservation priorities while those labelled in red are high priorities.

#### 4. Discussion

Previous studies have measured the evolutionary distinctiveness of species and phylogenetic community ecology in Madagascar. The phylogenetic diversity of most lemur communities was previously found to be either not significantly different from null expectations based on species richness, or more diverse than expected (Kamilar and Guidi, 2010; Razafindratsima et al., 2013). High phylogenetic diversity (overdispersion) was found in this study as well with the most comprehensive phylogeny, species representation, and number of communities. Previous assessments of lemur diversity used a subset of species, and were conducted at regional or grid-cell level analyses. Based on the evolutionary distinctiveness of 36 species and their distribution at the regional level, the northeastern humid forests and western dry

forests were identified as priority regions because of the high lemur phylogenetic diversity, distinctiveness and endemism (Lehman, 2006). Similarly, spatial analyses on a subset of 38 or 67 lemur species also identified the north, east and northwest as areas of high lemur species richness, phylogenetic diversity, endemism, and body mass evolutionary rates (Gudde and Venditti, 2016; Gudde et al., 2013). These results are upheld in the present study (Table 2), with the eastern PAs having high endangered lemur diversity and endemism. When ranking PAs based on functional diversity, however, the southwest region has more PAs with high rank than other regions. Considering the sum of ranks from multiple biodiversity metrics, forest productivity, heterogeneity, and forest loss, the southeast has the PAs with the highest median rank (316), followed by the northeast (320), while the southwest has the lowest median rank (380). The discrepancies among these studies emphasize that the priority ranking of PAs differs based on the metric used to evaluate them. Conservation biologists and policy makers must make decisions on what metrics have the greatest value to focus conservation efforts. Based on these results, I suggest that the sum of ranks based on diversity and habitat metrics be used to prioritize PAs because it represents the greatest representation of dimensions of biodiversity and habitat suitability, while avoiding collinear measures of diversity.

Early assessments of the conservation value of areas in Madagascar were based on the presence of charismatic, threatened “flagship” species (Wright and Andriamihaja, 2002), and later the maximal representation of species, especially those that are range restricted, across multiple taxonomic groups (Kremen et al., 2008). In 2005, the former president of Madagascar pledged to triple the amount of protected area, and protection was initiated for the priority zones identified by maximizing the diversity of multiple taxonomic groups. The system of protection varied among areas, including governance by the federal government through the Madagascar National Parks service, Special Reserves maintained by the forestry service, as well as locally-managed community-based conservation areas (Scales, 2014). Due to a *coup d'état* and subsequent political instability in 2009, the plans for enacting

**Table 1**

Correlations between the threatened species index and other diversity metrics, tested using linear mixed models on z-score transformed metrics, incorporating spatial autocorrelation and grouping by the region within which the protected areas occur to account for spatial effects.

Metrics	r	p
SR	0.93	0.0001
PD	0.38	0.0001
FD	0.20	0.036
PE	0.93	0.0001
EDGE	0.91	
ED	0.92	0
HEDGE	0.79	0
SOR	0.19	0.048
PHYSOR	0.48	0

r: Spearman's correlation coefficient, p: probability, SR: species richness, PD: phylogenetic diversity, FD: functional diversity, PE: phylogenetic endemism, EDGE: the sum of evolutionary distinctiveness and globally endangered scores, ED: the sum of evolutionary distinctiveness scores, HEDGE: heightened evolutionary distinctiveness and globally endangered scores, SOR: mean Sorenson's beta diversity index as a measure of species complementarity, PHYSOR: mean phylogenetic Sorenson's beta diversity index as a measure of phylogenetic complementarity.

**Table 2**

Rankings of the top 25 priority protected areas (PA) for lemur conservation based on the sum of ranks in each of seven metrics (for the complete list of 100 PAs and all metrics evaluated, see the Supplementary information, Appendix B).

PA	Priority rank	Sum of ranks	TSI	PD	FD	HEDGE	SOR	PFL	NPP	ALT.SD	Region <sup>a</sup>
Corridor Fandriana-Marolambo	1	179	28	10	6	55	58	17	15	18	SE
Ambatofotsy	2	203	98	18	20	15	100	5	7	38	NE
Marotandrano	3	204	25	22	3	47	38	28	22	44	CH
Tsaratana Future SAPM	4	228	57	41	40	50	47	11	35	4	NW
Anjozorobe Angavo	5	231	18	49	27	86	5	9	18	37	NW
Manongarivo	6	233	31	5	7	74	82	29	33	3	NW
Tsaratana	7	235	35	14	30	80	52	21	36	2	NW
Complexe Kalabenono	8	239	56	40	39	49	53	4	34	20	NW
Midongy du Sud	9	244	26	20	51	41	80	23	19	10	SE
Forêt Tsitongambarika	10	250	47	16	77	34	67	13	28	15	SE
Bemarivo	11	258	58	9	4	63	10	39	51	82	NW
Extension Ankodida Tsimelaha	12	260	64	44	2	39	2	74	66	33	SW
Corridor Ankeniheny Zahamena	13	263	5	34	55	93	26	19	12	24	NE
Ambohidray	14	278	46	35	53	40	8	44	24	74	CH
Bemanevika	15	279	51	11	72	44	45	53	43	11	NW
Montagne des Francais	16	282	70	29	26	1	87	20	63	56	NW
Ambatovaky	17	283	17	28	58	82	49	26	21	19	NE
Mangabe	18	284	13	17	78	94	23	1	1	70	CH
Maromizaha	19	284	9	31	91	97	11	2	3	49	NE
Masoala	20	286	19	3	28	62	77	75	27	14	NE
Mananara Nord	21	289	10	13	41	52	69	45	17	52	NE
Ranomafana	22	294	3	7	45	81	63	60	9	29	SE
Mangerivola	23	296	6	30	92	91	20	34	16	13	NE
Mantadia	24	296	14	21	87	92	19	24	14	39	NE
Sahafina	25	298	78	33	61	12	62	59	5	66	NE

TSI: threatened species index (not used in sum of ranks), PD: phylogenetic diversity, FD: functional diversity, HEDGE: the sum of heightened evolutionary distinctiveness and globally endangered scores, SOR: the mean Sorenson's index of beta diversity, NPP: the net primary productivity, PFL: the percent forest loss between the years 2000 and 2014, ALT.SD: standard deviation of elevation.

<sup>a</sup> Region within which the PA is located, as follows: northeast (NE), northwest (NW), southeast (SE), southwest (SW), and central highlands (CH).

the previous conservation vision stalled. While many of the areas have been delineated and local community conservation associations formed, on-the-ground efforts in many remote areas have not been pursued (Scales, 2014).

In 2013, an updated conservation status assessment of all lemurs revealed that 93% of known species were at risk of going extinct (Schwitzer et al., 2014). This led lemur specialists to advocate a PA prioritization scheme that ranked PAs by the richness of their lemur communities, weighted by the endangerment status of those lemurs (Schwitzer et al., 2013; Schwitzer et al., 2014). Plans for realizing conservation action between 2013 and 2016 were outlined and budgeted, with clear goals and measures of evaluating success. In total, it was estimated that 7.6 million US dollars (USD) would be needed to implement the action plan. In future plans for conservation action, the results of this study illustrate that a multidimensional approach to priority planning should be implemented. To do so, researchers actively working on lemur surveys and quantifying threats to lemurs and their habitat should pool the latest data and standardize them for the most accurate, updated assessments of species diversity and threat in PAs.

The value of PAs for people, both at the local stakeholder and the national government scales, must be assessed and compared to the valuation based on biodiversity. Parks can have great benefits for local communities and nations, drawing international recognition and currency. There are two natural and one cultural UNESCO World Heritage Sites in Madagascar, including the Tsingy de Bemaraha National Park in the northwest and the Marojejy National Park in the northeast, both of which are high priority areas based on lemur diversity. Revenue from tourism was estimated at 400 million USD in 2008, and one PA in southeast Madagascar, Ranomafana National Park, has brought in over 1 million USD annually both through tourism and research (Wright et al., 2014). The economic benefits of PAs do not always offset the costs to local stakeholders, however, leading to high deforestation (Desbureaux et al., 2016). Data on the revenue generated by the PAs from tourist and research activities should be combined with information on the socio-cultural and utilitarian use values of the PAs for local stakeholders to further evaluate the proximal values of PAs for people.

This study focused on taxonomic, phylogenetic and functional dimensions of lemur biogeography and community ecology to assess the priority PAs for lemur conservation. Past biodiversity loss has been quantified using hindcasting of the presumed pre-human distribution of species and communities and the rate of suitable habitat loss, illustrating that ~40% of species may have gone extinct due to habitat loss (Allnutt et al., 2008). Also, the present distribution of species may fail to represent their distributions under future climate change scenarios. The ranges of most species are predicted to change in the future, some expanding while most contract (Brown and Yoder, 2015). Forecasts of species distributions, their suitable climates and forest cover can be used to predict future community composition using generalized dissimilarity modelling (Ferrier et al., 2007) and subsequent research should apply these techniques to assess the predicted value of PAs for lemurs in the future. Further, lemurs are only one taxonomic group of high conservation concern; the value of PAs for plants, herpetofauna, invertebrates, birds, mammals and other groups should be assessed in the same framework presented here to further evaluate the value of PAs for whole ecosystems.

## 5. Conclusions

The results of this study reveal that previous conservation priority ranking schemes based on the richness of threatened lemur species may undervalue PAs with high diversity in other measures, such as the evolutionary history, functional diversity, habitat productivity and level of anthropogenic threat. By combining data on multiple dimensions of biodiversity, I ranked PAs objectively, capturing different aspects of diversity and endemism as well as habitat characteristics and threat level. Lemur diversity was related to habitat characteristics that measured environmental productivity and heterogeneity as well as forest cover. This result facilitates assessment of areas for future conservation even with missing data on lemur community composition, solely based on remotely sensed habitat features. High habitat loss has occurred in the PAs with the highest combined diversity, revealing that the evolutionary history and functional diversity of PAs is eroding.

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## Appendix A. Supplementary data

Detailed methods, raw data and sources associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.biocon.2016.12.028>.

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