LEMUR SPECIES-HABITAT RELATIONSHIPS AT MULTIPLE SPATIAL SCALES IN RANOMAFANA NATIONAL PARK, MADAGASCAR

by

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I certify the following:

1. Does this proposed MP involve human subjects research? ___ Yes __x__No
   a. If yes, has an approved IRB protocol been obtained? ___ Yes ____No

2. Does this proposed MP involve the use of animals in research? ___ Yes __x__No

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Abstract

Lemur populations are threatened by many factors, but are most impacted by habitat loss, fragmentation, and alteration. Studies have shown that there is a lag time between habitat disturbance and species response. Thus, more data is needed on long-term relationships between forest change and lemur populations to fully understand how anthropogenic disturbances affect lemurs over time. To bridge this data gap, this study evaluates lemur biodiversity and abundance in three levels of forest disturbance (heavily logged, selectively logged, and pristine forest) at multiple spatial scales. This project 1) isolates which specific microhabitat and landscape variables are important for different lemur species 2) evaluates if the habitat is significantly different between the three forest sites, and 3) evaluates if lemur biodiversity is significantly different between recovering and pristine forests. These results will not only help determine species-specific habitat requirements for critically endangered lemurs, but also contribute to previous data sets on recovering forest monitoring.

Executive Summary

There is a lack of data on the long-term relationships between forest change and lemur presence and abundance. To bridge this data gap, this study evaluates lemur composition in three levels of historical forest disturbance at multiple spatial scales. This study was conducted in central Ranomafana National Park (RNP) between May 31st and July 25th, 2017. RNP is home to 12 lemur species, 7 of which are diurnal and range from near threatened to critically endangered status. RNP is also home to one unique species, the Golden Bamboo Lemur (*Hapalemur aureus*), which is not found elsewhere in Madagascar.

Our study sites were Talatakely (heavily logged), Vatoharanana (selectively logged), and Valohoaka (pristine forest). We established 26 plots that were 400 m^2 to evaluate the microhabitat at each site. We used the point-centered quarter method to collect information on tree diameter at breast height (DBH), canopy cover, tree height, percent ground cover, crown diameter, tree species, tree phenophase, number of dead trees, and number of bamboo stems in each sub-plot. We revisited each plot to search for lemurs and recorded the number and species when found. Later, we used ArcMap to analyze the distance between research plots and landscape features such as distance to nearest camp, distance to main trail, and distance to forest edge.

This study addresses the following research questions:

1. What is the relationship between lemur species composition/abundance and habitat at the *microhabitat* scale in RNP?
    a. Is there a significant difference in *microhabitat* characteristics between a heavily logged site (Talatakely) and lightly disturbed sites (Vato and Valo)?
    b. Is there a significant difference in *microhabitat* characteristics between a heavily logged site (Talatakely), a minimally logged site (Vato), and a pristine site (Valo)?
2. What is the relationship between lemur species composition/abundance and habitat at the *landscape* scale in RNP?
    a. Is there a significant difference in *landscape* characteristics between a heavily logged site (Talatakely) and lightly disturbed sites (Vato and Valo)?

   b. Is there a significant difference in *landscape* characteristics between a heavily logged site (Talatakely), a minimally logged site (Vato), and a pristine site (Valo)?

3. What is the relative strength of the relationships between lemur species composition/abundance and habitat at two spatial scales?
4. Is there a significant difference in lemur species composition/abundance between Tala, Vato, and Valo?

I used Mantel's tests (Mantel 1967) to determine how variations in lemur species richness related to variations in habitat variables when holding all other landscape, microhabitat, and geographic variables constant. I then calculated this iteratively for each individual variable, for all 7 diurnal lemur species, across all 26 plots. I then used ANOVA and t-tests to determine if there was a significant difference in habitat variables or lemur composition/abundance between the three sites.

The results of this study show that the microhabitat and landscape characteristics between Tala, Vato, and Valo are significantly different from each other. Some habitat factors have stayed the same since past studies over a decade ago, while some habitat factors have begun to shift. Despite these habitat differences, lemur abundance and composition do not significantly differ between sites. It is most likely that the habitat factors that most influence their presence or abundance do not differ between sites.

Three of the seven diurnal lemur species in RNP showed significant relationships with different habitat factors, which appeared to be driven by their specialized diets. The golden bamboo lemur (*H. aureus*) was significantly related to their main food source, bamboo. The black and white ruffed lemur (*Varecia vagiegata*) was significantly related to tree density, canopy cover, and tree DBH. These are all factors that affect the fruit production of their food source trees. The one exception is the negative relationship between *E. rubriventer* and distance to camp or research building. At this time we do not have enough evidence to make any assumptions about why this negative relationship occurs. But it is clear that some aspect of anthropogenic presence is driving *E. rubriventer* further from human-occupied areas.

Introduction

Madagascar is one of the leading biodiversity hotspots on Earth (Myers et al. 2000). As of 2000, it contained 84 endemic mammal species, most of which are lemurs. Upwards of 94% of all lemur species are considered threatened (Schwitzer et al. 2014), mostly due to habitat loss and fragmentation (Richard & Sussman 1975). In 1991, Ranomafana National Park (RNP) was established after the discovery of the golden bamboo lemur in hopes of helping conserve it and other lemur species. RNP contains areas of pristine forest, partially logged forest, and stands of heavily logged forest. Yet, there is no long-term study to evaluate how the forest is recovering from past disturbance. Additionally, there is no long-term study evaluating how different lemur species prioritize these different forest types. It is essential to continue to monitor how lemurs are using the habitat, especially a recovering habitat, to identify which habitat factors best support their populations. To fill this data gap, I evaluated the relationships between lemurs and their habitat in RNP using a multi-scale approach, in an area that has not been comprehensively assessed since 2008. This data delineates species-specific habitat requirements, while also continuing to monitor a recovering forest. This is valuable not only for properly managing currently protected areas, but also for identifying future protected areas.

Lemurs are the most threatened mammal group in the world (Schwitzer et al. 2014). They are threatened by illegal bushmeat hunting, exotic pet trade, increase in diseases, extensive habitat loss, and habitat fragmentation (summarized in Richard and Sussman 1975). In fact, Madagascar has lost 80-90% of its forests since human colonization on the island (Myers et al. 2000; Harper et al. 2007). Increased logging and slash-and-burn agriculture (AKA tavy) has increased forest edges and fragments (Chen et al. 1992). These threats are all caused by humans, making more immediate anthropogenic impacts on lemur populations a relatively well-studied subject (Brown & Gurevitch 2004; Herrera et al. 2011; Bublitz et al. 2015; Dunham et al. 2008; Ganzhorn 1995).

Moreover, studies have shown that there is a lag time between habitat disturbance and species response (Worman & Chapman 2006; Brooks et al. 1999; Newmark et al. 2017). Thus, more data is needed on long-term relationships between forest change and lemur populations to fully understand how anthropogenic disturbances affect lemurs over time. This information is imperative for creating effective conservation management plans by showing a trend in biodiversity change over time, as opposed to short-term and seasonal fluctuations (Wright et al. 2012). Recognizing how different species are affected by and adapt to anthropogenic effects helps conservationists better understand how to implement successful species-specific conservation plans. This also helps us monitor how species biodiversity changes in a forest recovering from being logged.

Past studies have evaluated forest habitats at different successional states, before and after logging, while also surveying different levels of logging intensity. For example, in 1995 Ganzhorn researched low-intensity logging in western Madagascar and found that logging exposed trees to more sunlight which resulted in a higher protein content (Ganzhorn 1995). Therefore the leaves were a higher quality, which would greatly benefit folivores. Ganzhorn also found that fruit production increased, which would be beneficial for frugivores. Overall, Ganzhorn found more lemurs of all species in the low-intensity logged areas than in the pre-logged state, but found a decline in lemurs in high-intensity logging areas.

Then, between 2002 and 2006, Johnson et al (2005) investigated how biodiversity was affected by different levels of anthropogenic disturbance in four corners of RNP (Figure 1) which have different levels of habitat disturbance. They conducted a comprehensive assessment of diurnal primates, nocturnal primates, micro mammals, botanical plots, human disturbance, bird surveys, insect surveys, and chameleon surveys (unpublished report). They found that the southern zone (Figure 1), which is comprised of undisturbed, pristine forest, contained the richest plant biodiversity. The southern zone also contained *Varecia variegata* (black and white ruffed lemur) abundantly, which are typically only found in undisturbed forest (Irwin et al. 2005). There was a lack of *Prolemur simus* (greater bamboo lemur) at all sites in RNP, likely due to a lack of their main food source, bamboo. *Hapalemur aureus* (golden bamboo lemur) was observed in the southern and central zones (Figure 1) in 2005, but not observed in 2006.

Similarly, Herrera et al. (2011) surveyed a heavily logged site (Talatakely) and a selectively logged site (Vatoharanana) in the central section of RNP (Figure 2) to assess how habitat disturbance affected lemur populations. They used circuitous survey routes on pre-existing trails where possible, and found lemur species had varying abundances at each site. *Eulemur rufifrons* (red-fronted lemur), *Varecia variegata* (black and white ruffed lemur), and *Avahi peyrierasi* (Peyrieras' woolly lemur) were found significantly more frequently in the selectively logged site than in the heavily logged site. This is consistent with Ganzhorn's results overall. However, *Microcebus rufus* (brown mouse lemur) was found at a greater abundance in the heavily logged site than the selectively logged site. Then three species (*Eulemur rubriventer* – red-bellied lemur, *Propithecus edwardsi* - Milne-Edwards' sifaka, *Hapalemur griseus* – gentle grey bamboo lemur), showed no statstically significant difference between the two sites.

This demonstrates that each lemur species requires particular microhabitat factors, which affects their distribution and abundances differently (Rendigs et al. 2003; Irwin et al. 2005; Wright et al. 2012). Therefore, a microhabitat assessment is imperative for studying the relationship between lemurs and their environment.

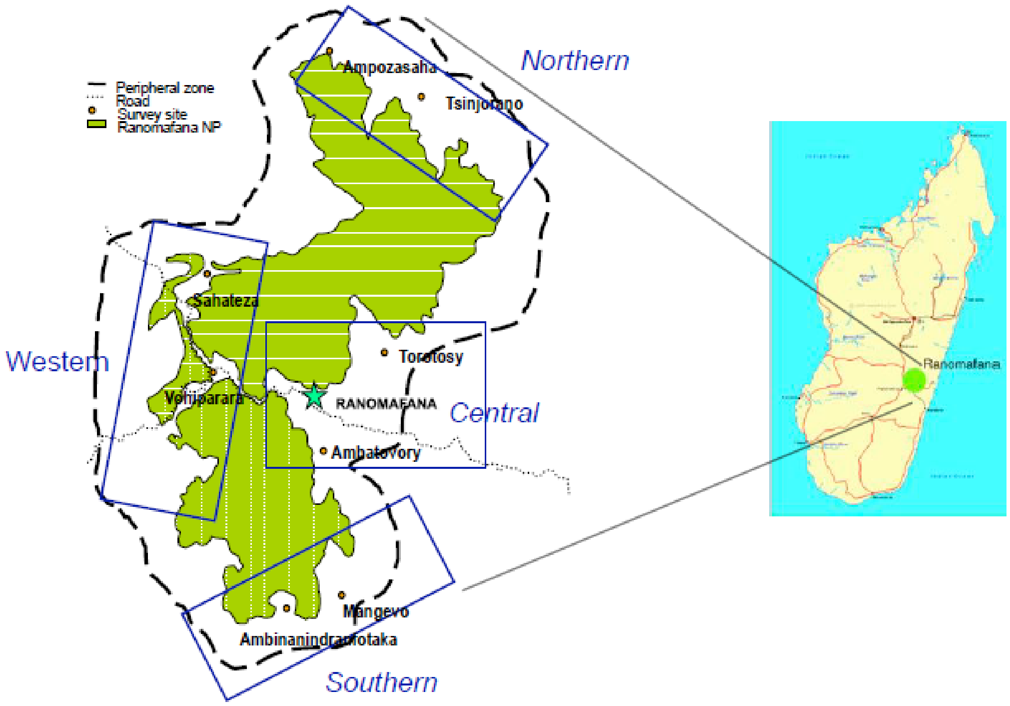


Figure 1: Field sites studied in 2005 by Johnson et al. in Ranomafana National Park, Madagascar (unpublished report, Johnson et al 2005).

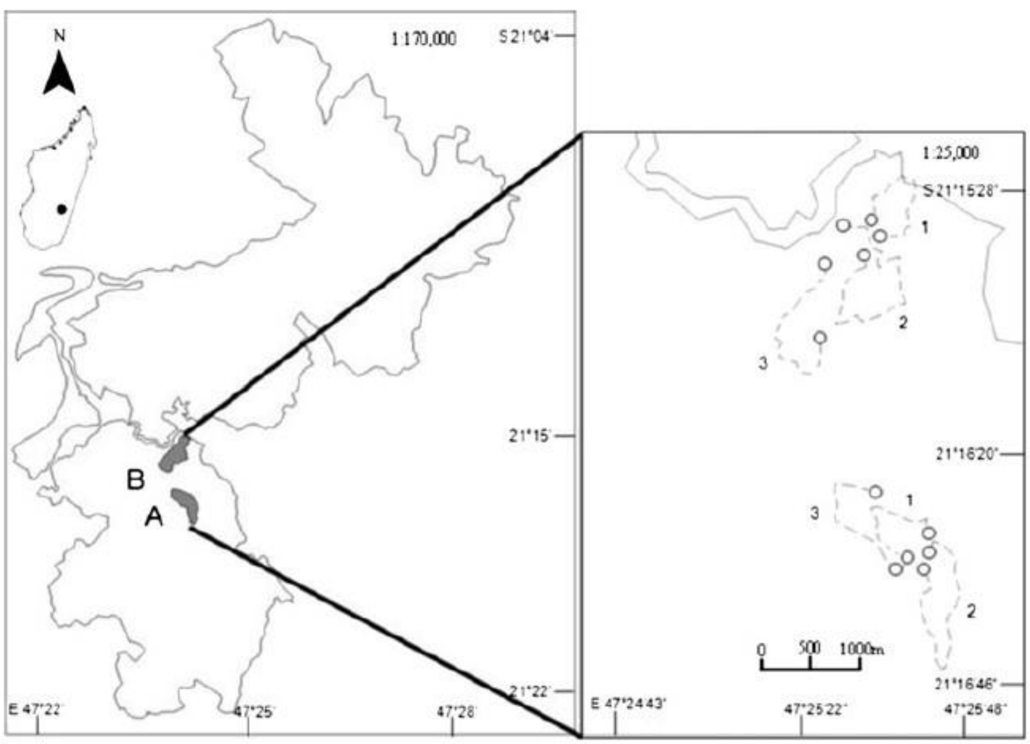


Figure 2: Field sites studied in 2008 by Herrera et al. in Ranomafana National Park, Madagascar (Herrera et al. 2011) . (A = Vatoharanana, B = Talatakely)

My study focuses on similar objectives to that of Johnson et al (2005) and Herrera et al (2001) by assessing lemur biodiversity change with habitat and different levels of disturbance. However, I focus only on diurnal species, I introduce different methodology, and new habitat variables at both the microhabitat and landscape-scale. By conducting a full habitat analysis at multiple spatial scales, I sought to isolate the relative strength of relationships among attributes of lemur biodiversity and a variety of habitat components. I also introduce new methodology to address Crouse et al.'s (2015) statement that "current primate survey methods (such as line transects) may not yield accurate assessment." Therefore, I instead use random point methodology to attempt to mitigate potential issues of auto-correlation that tend to arise by surveying on a transect. This approach allows me to assess the success of using random point surveying on lemur species.

This study investigates relationships of multi-scale forest attributes and lemur populations at the same sites studied by Herrera et al in 2008, but also adds an additional site, Valohoaka (Figure 3). Valohoaka is unique from Vatoharanana and Talatakely since it is pristine forest that was never logged. Talatakely was previously intensely logged, and Vatoharanana was selectively logged (Wright et al. 2012). This creates a three-part analysis of anthropogenic impact where Talatakely would be considered most impacted, Valohoaka would be considered least impacted, and Vatoharanana would be somewhere in-between. Therefore, a secondary result of this research is to continue to monitor biodiversity in a recovering site and a minimally disturbed site since it was last comprehensively assessed by Herrera et al in 2008, while adding the component of comparing it to a pristine site.

Finally, this research is necessary to understand primate response to anthropogenic effects over time. In particular, this provides a framework for long-term data collection on lemur responses to forest change and recovery by building on previous habitat disturbance studies in this study area. Monitoring population dynamics is an important factor for determining species extinction risk (Glessner & Britt 2005). In conclusion, this study addresses the following research questions:

5. What is the relationship between lemur species composition/abundance and habitat at the *microhabitat* scale in RNP?
    a. Is there a significant difference in *microhabitat* characteristics between a heavily logged site (Talatakely) and lightly disturbed sites (Vato and Valo)?
    b. Is there a significant difference in *microhabitat* characteristics between a heavily logged site (Talatakely), a minimally logged site (Vato), and a pristine site (Valo)?
6. What is the relationship between lemur species composition/abundance and habitat at the *landscape* scale in RNP?
    a. Is there a significant difference in *landscape* characteristics between a heavily logged site (Talatakely) and lightly disturbed sites (Vato and Valo)?
    b. Is there a significant difference in *landscape* characteristics between a heavily logged site (Talatakely), a minimally logged site (Vato), and a pristine site (Valo)?
7. What is the relative strength of the relationships between lemur species composition/abundance and habitat at two spatial scales?
8. Is there a significant difference in lemur species composition/abundance between Tala, Vato, and Valo?

Study Area

The study was conducted in three sites of Ranomafana National Park (RNP): Talatakely (Tala), Vatoharanana (Vato), and Valohoaka (Valo) (Figure 3). "RNP is located between 47º 18' and 47º 37' east, and 21º 02' and 21º 25' south" (Balko & Underwood 2005). RNP is comprised of 41,600 hectares of mid-altitude forest ranging from 500 – 1500 m (Mittermeier et al. 1992; Wright 1995). RNP's mountainous landscape and sub-montane rain forest provides a variety of different forest niches (Wright 1995). RNP is home to 12 lemur species (Appendix I): 3 critically endangered, 3 endangered, 3 vulnerable, 1 near threatened, and 1 that is data deficient (IUCN Red List; Wright 1995). Of these 12 species, 7 are diurnal and 5 are nocturnal.

Tala, Vato, and Valo vary in their accessibility, and popularity with tourists. Tala is directly adjacent to the park entrance and is frequented by tourists daily. Hiking into Tala is only about 10 to 15 minutes from the entrance, but the trail system extends as far as an hour from the entrance (~2 km by trail). Vato camp is about 2 hours from the entrance (~7 km by trail), and Valo camp is about 3 hours from the entrance (~10 km by trail). These estimates are based on average tourist or researcher hiking speed as opposed to that of local field technicians who know the trails better and hike much quicker. Valo is designated as a research only site, whereas Vato is frequented by both researchers and tourists.

The three sites also vary in their level of past disturbance due to logging. Tala was heavily logged from 1986 to 1989, Vato was selectively logged of ~1000 trees between 1987 and 1988, and Valo was never logged (Balko & Underwood 2005; Wright et al. 2012). Finally, the three sites varied in their level of anthropogenic impact. Many plots contained foot paths where tour guides and tourists travelled off path to see lemurs. This was especially noticeable in Tala, where we not only saw tourists using some footpaths, but we also saw recently dropped/discarded litter on other footpaths. Foot paths in Vato or Valo were rare. Any foot paths we came across at these sites were overgrown transects from past studies. Though these paths were not maintained, they were still clearly used to cut between main trails as stated by local field technicians.

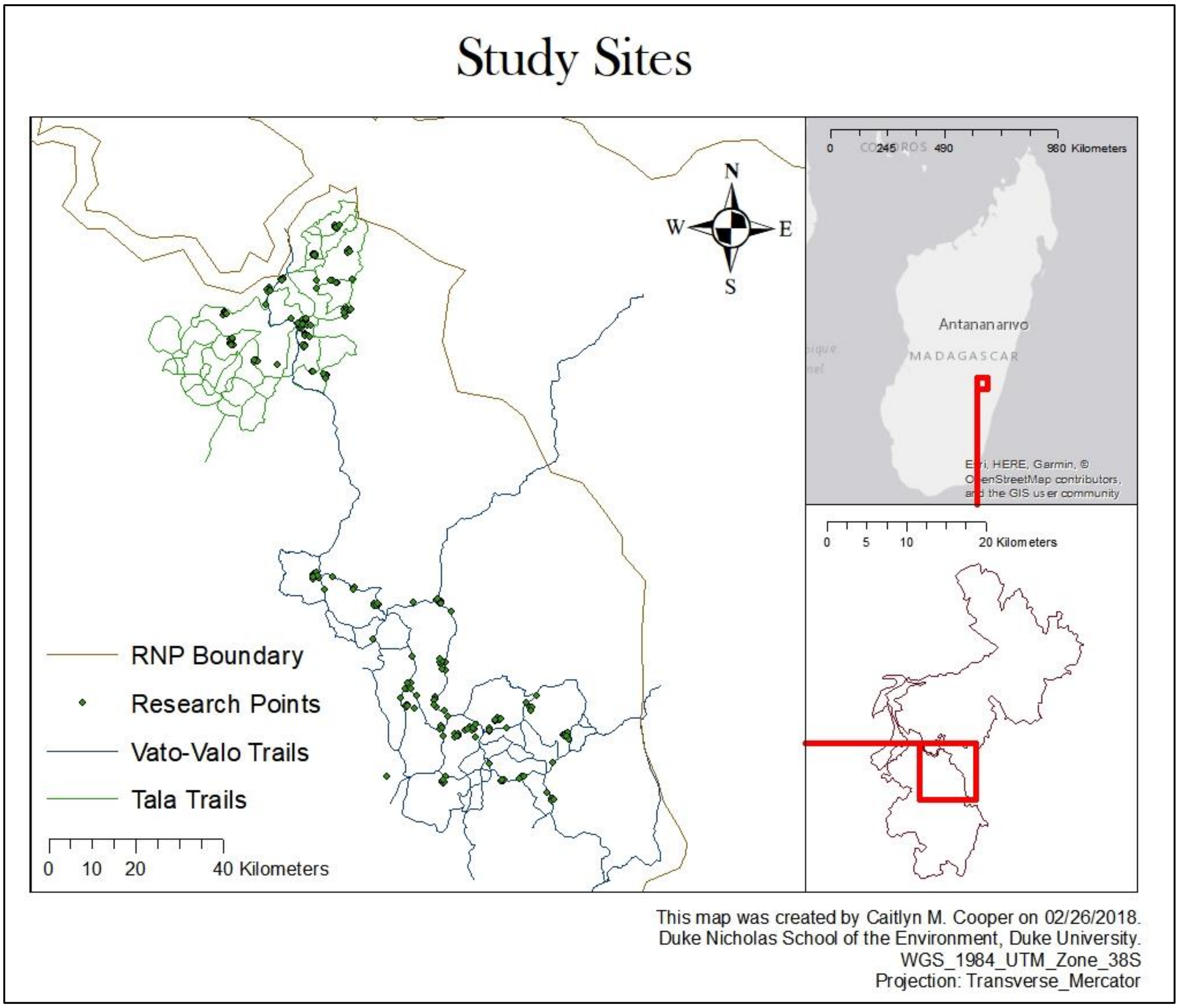


Figure 3: Field study site area in Ranomafana National Park, Madagascar. Research points indicate all plots, observed lemurs, or signs of anthropogenic disturbance. The top right inset map shows location of RNP in Madagascar. The bottom right inset map shows the research location within RNP. See Appendix Figure 13 for the distinction between Vato and Valo.

Project Methods

Data was collected between May 31st and July 25th, 2017 between the hours of 8 AM and 5 PM (East Africa Timezone). We spent 17 field days in Tala, 9 field days in Valo, and 9 field days in Vato. We used ArcGIS to plot random points throughout the trail matrix. Once in the field, if points were not accessible due to difficult terrain (i.e. severely steep slopes), adjacent points were chosen at varying distances from the main trail (ranging from 2 to 137 meters). The random points' latitude and longitude became the location of the center point in the microhabitat plots.

Fifteen plots were established in Tala, but two of these plots were eliminated in the analysis since they were directly adjacent to other plots. Eight plots were established in Valo and five plots were established in Vato. The original intention was to group Valo and Vato plots into one "minimally disturbed" category, which would have created thirteen plots for each disturbance category (heavily disturbed and minimally disturbed). However, the three sites were split up in the analysis to create a greater understanding of the three levels of disturbance present (heavily disturbed, minimally disturbed, and pristine/undisturbed).

Microhabitat Assessment

For each plot we recorded the site, date, and start/end time of data collection. We also recorded ancillary data such as weather at the start and end of data collection. We used the point-centered quarter method for the microhabitat assessment (Balko & Underwood 2005). The plots were 20-meter by 20-meter around the center point and split into four sub-plots. GPS coordinates were taken of all plot corners and plot center with a Trimble Juno 3B GPS unit. We collected microhabitat information on tree diameter at breast height (DBH), canopy cover, tree height, percent ground cover, crown diameter, tree species, tree phenophase, number of dead trees, and number of bamboo stems in each sub-plot.

We measured the tree DBH (at 1.3-meter height) of each tree with a DBH > 10cm. We used a densiometer to find canopy cover in each sub-plot. We measured canopy cover in all four cardinal directions and averaged the four values. Tree height was visually estimated since vegetation was too dense to use a clinometer. Percent ground cover was estimated using Figure 4. Though this figure is normally used to roughly estimate crown density, we considered it a consistent estimator for ground cover as well. Crown diameter was estimated at the widest part of the crown, and at the width perpendicular to the widest part of the crown. These two measurements were averaged to find crown diameter for each tree. Canopy cover, tree height, percent ground cover, and crown width were measured or estimated by the same technicians in all plots for consistency of measurements. Canopy cover, tree height, percent ground cover, crown width, and tree DBH were averaged across all four sub-plots.

We counted the number of bamboo stalks in each plot where possible. This is an important habitat variable to record since RNP is home to three bamboo lemur species (*Prolemur simus* – greater bamboo lemur, *Hapalemur aureus* – golden bamboo lemur, *Hapalemur griseus* – gentle grey bamboo lemur), and bamboo is most of their diet. The three species of bamboo that we encountered were known locally as *volosy* (*Cathariostachys madagascariensis*: Poaceae – Also called "Giant Bamboo"), *volotsangana* (*Bambusa madagascariensis*: Poaceae), and *tsimbolo/tsimbolovolo* (*Cephalostachyum viguieri*[1]: Poaceae). *Volosy* and *volotsangana* are large-culm bamboo stalks, whereas *tsimbolo* is an understory vine (King et al. 2013; Cadle

[1] Alternate spelling: *Cephalastachium vigueri*

2014). Therefore, we were only able to count the number of *volosy* and *volotsangana* bamboo stalks, since vines were impossible to count.

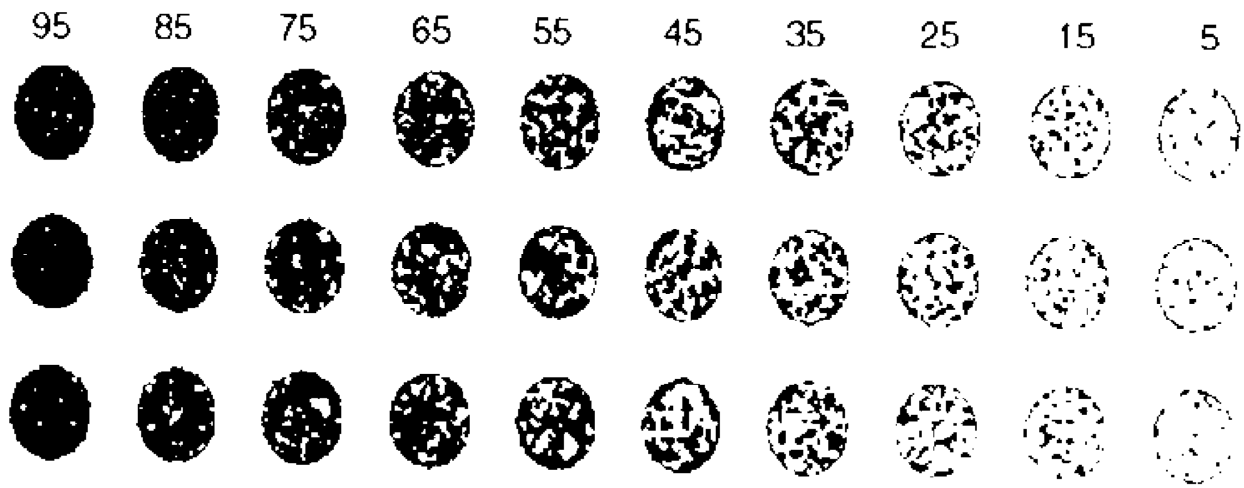


Figure 4: This image was used to estimate percent ground cover in each sub-plot. [2]

The most comprehensive study on the diet of the three bamboo lemurs found in RNP shows that all three species consume parts of *volosy* (Tan 1999). RNP contains only two remaining individuals of the critically endangered *P. simus's*, whose diet is 95% *volosy* (Tan 1999). Also, *H. aureus's* diet was 78% *volosy*, and *H. griseus's* diet was 72% *volosy* (Tan 1999). Current literature hints that these species also feed on *volotsangana*, but it does not specifically mention which species, or what percentage of their diet is made up of *volotsangana* (Ballhorn et al. 2016). This is likely because Tan et al's (1999) study site included only Tala, but not Vato or Valo. *Volosy* is primarily found at elevations ranging from ~600 – 1200 meters (King et al. 2013) whereas *volotsangana* is only found at elevations higher than 1000 meters. Therefore, *volotsangana* is not found at Tala and would not have been evaluated for its importance in

[2] USDA Field Methods for Forest Health (Phase 3) Measurements Field Guide, Section 23.3 Crowns: Measurements and Sampling, Crown Density-Foliage Transparency Card

bamboo lemurs' diet. However, we include *volotsangana* bamboo in our analysis anyway as it is likely eaten by bamboo lemurs to some degree, thus making it worth measuring.

Tree species were identified by team botanists. Sometimes a small notch was made in tree bark to help with accurate identification. Tree phenophase was identified as whether the tree was fruiting, flowering, or neither. The microhabitat was only assessed once at each plot. Since we surveyed during the same dry season, any change in the variables over the period of data collection was expected to be negligible.

Landscape Analysis

I used ArcMap (version 10.4.1) to analyze landscape habitat variables including each plots' distance to the nearest campsite/research building, main trail, main forest edge, elevation and cultivated patch edge. In some cases, a cultivated patch was present within the forest matrix, and was considered the edge of the habitat (Appendix, Figure 14). Though forest was present beyond the cultivated patch, it was considered unlikely for lemurs to go around the patch due to its large size. Therefore, we included the distance to this patch as a separate variable that is essentially a proxy for distance to forest edge. I used the coordinate system WGS 1984 UTM Zone 38S. Elevation was obtained from a 90-meter resolution digital elevation model GeoTIFF (Watkins, D. SRTM Tile Grabber)

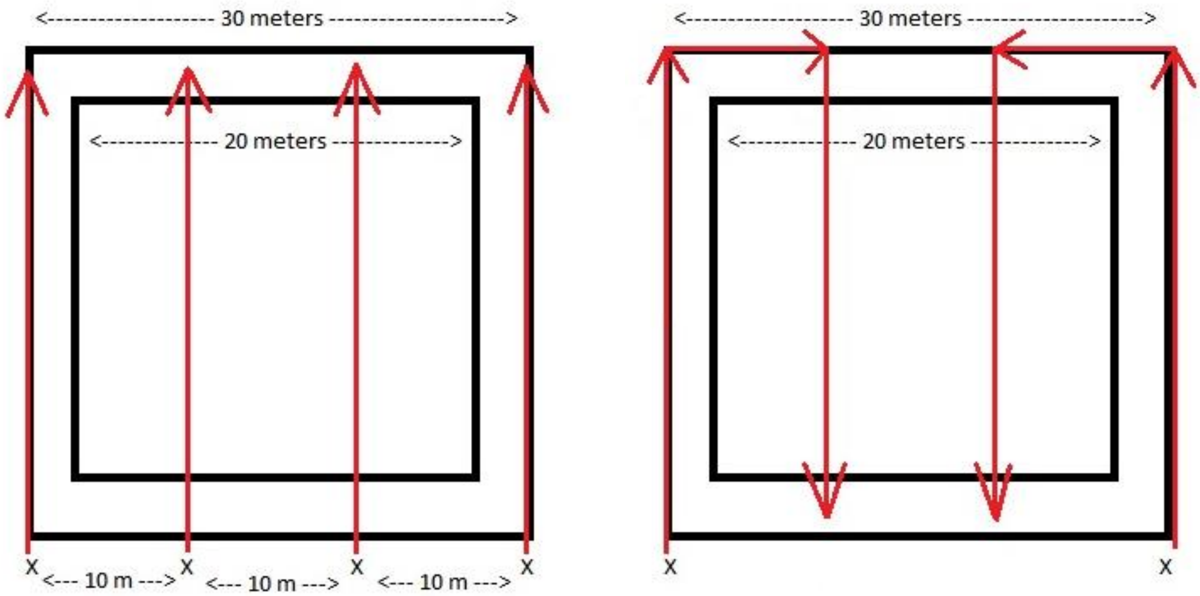
Signs of Anthropogenic Impact

We also recorded signs of anthropogenic impact or presence both incidentally, and in each 20-meter by 20-meter microhabitat plot. We recorded the number of animal traps, domestic cattle dung, cut trees, signs of fire, and number of trees with stripped bark. Any signs of human presence were compiled with corresponding GPS coordinates and photos, then given to park management.

Lemur Surveys

Each microhabitat plot was assessed for lemur presence when initially setting up the plot. Then, each plot was revisited 7-9 times to survey for lemurs – the maximum number of revisits time allowed during the 56-day field season. We varied the time of day that each plot was visited to avoid any bias with a particular time of day. We collected data on the number of lemurs present, the lemurs' species, GPS location of lemur, and method of detection (i.e. visual, heard call, found signs of presence) at each plot. Identifying signs of lemur presence down to species was only realistically feasible for the three bamboo lemurs since they each consume different parts of the bamboo plant. We also recorded lemur activity at time of survey (i.e. sleeping, feeding, moving, etc), their sex, and age group (adult, sub-adult, juvenile, infant) when possible. Any lemur found incidentally on the trail when travelling between plots was also recorded.

When visiting the plot, our team of four was spaced about ~10 meters apart and slowly crossed the plot for 10 minutes of silent observation (Figure 5a). With this spacing, we covered an additional 5 meters on all sides of the 20-meter by 20-meter plot, creating a 30-meter by 30-meter area of observation. The row of technicians would walk a few steps and pause to make observations, then walk a few steps and pause, repeatedly, to cut down on the amount noise made by walking through the foliage, which made it easier to hear and identify lemurs in the trees. If lemurs were found in the first 10 minutes of observations, then the timer was paused to gather data on the species present. After observation on the lemur was completed, then the timer was then restarted, and the remainder of the observation area was surveyed for additional lemurs until the full 10-minute period had elapsed.



A **B**

Figure 5: This shows the way plots were surveyed with a team of four technicians (a) and a team of two technicians (b) when crossing the 20-meter by 20-meter research plots. Technicians are indicated by an "x" and their survey path is indicated by red arrows.

Towards the end of the field season the team split up to maximize the number of observations for the few remaining plots. The teams of two conducted lemur observations for 20 minutes instead of 10 minutes, to account for the change in sampling effort and additional time needed to cover the same amount of area with fewer technicians (Figure 4b).

Data Analysis

All statistical analysis was conducted on research plot data and did not include incidental lemur sighting data. Since we did not collect habitat data around incidental lemur sightings, we could not make assumptions about the relationships between those lemurs and their habitat.

Incidental lemur data was only used to get a general idea for lemur composition across study sites.

I used Mantel's tests (Mantel 1967) to determine how variations in lemur species richness related to variations in habitat variables when holding all other landscape, microhabitat, and geographic variables constant. I then calculated this iteratively for each individual variable, for all 7 diurnal lemur species, across all 26 plots. Since there were so few categories for signs of anthropogenic presence, they were grouped in with the landscape scale variables (Table 1). There was too little data on cut trees, therefore we did not run our analysis on this variable.

Mantel's tests also allow us to ask questions about the variables in a more holistic way by grouping all variables from a particular category together (i.e. all microhabitat variables) as opposed to looking at each variable individually. Therefore, I used Mantel's tests to answer the following questions:

- How are variations in lemur richness related to differences in microhabitat (i.e. all microhabitat variables) holding landscape and geographic variables constant?
- How are variations in lemur richness related to differences in landscape (i.e. all landscape variables) holding microhabitat and geographic variables constant?
- How are variations in lemur richness related to differences in geography (i.e. latitude and longitude) holding microhabitat and landscape variables constant?

Mantel's tests were conducted using R statistical software, version 3.2.4 (Revised 2016-03-16 r70336). I used the "Ecodist" package, version 2.0.1, (Goslee and Urban, 2006) which contains "Dissimilarity-Based Functions for Ecological Analysis" to analyze spatial data. I used Bray-Curtis distance coefficients to create a lemur species composition dissimilarity matrix. I used Mahalanobis distance coefficients to create dissimilarity matrices for microhabitat and landscape variables. I relativized by column maximum for the species data analysis, which mitigates for species that might be more abundant than others.

Table 1: Habitat variables grouped in each category for the large matrix Mantel's tests.

Landscape Variables	**Microhabitat Variables**	**Geographic Variables**
• # Zebu droppings • Distance to main trail (m) • Distance to camp/research building (m) • Distance to main forest edge (m) • Distance to cultivated patch (m) • Elevation (m)	• Tree diversity (# species per plot) • Average canopy cover (%) • Average crown width (m) • Average tree height (m) • Average tree DBH (in) • Tree abundance (# trees per plot) • # dead trees (per plot) • Average ground cover (%) • # bamboo stems • # flowering trees • # fruiting trees	• Latitude • Longitude

Mantel's tests were also done on presence-absence data of lemur species at each site. This was conducted in the same way as lemur species composition. However, instead of taking lemur abundance into account, this test simply analyzed a matrix of 1's (present) and 0's (absent). Since all species presence values have equal weight, I did not relativize by column. The importance of this test was summarized nicely by Gibson (2011): "Statistical models that relate the presence and absence of individual species to environmental variables (e.g. soils, climate and topography) can be used to predict their potential distributions … as well as assist in delineating their specific habitat requirements." Therefore, presence-absence analysis helps amplify species-habitat relationships by giving all species equal weight in the calculations.

To test for differences between Tala, Vato, and Valo as three separate sites, I did an ANOVA for each microhabitat variable and lemur diversity. I calculated site lemur diversity using the Shannon-Weiner diversity index. I used the Shapiro-Wilks test to check for normality, and then used the non-parametric Kruskal-Wallis test for variables that were non-normal. To test for differences between Tala and Vato/Valo as two separate sites, I conducted a two-tailed t-test. Again, to test for normality I used the Shapiro-Wilks test, then used the Wilcox-Mann-Whitney-U-test for variables that were non-normal. To gain a better understanding of how all habitat variables were associated, I calculated Pearson product-moment correlations among habitat features.

Results

Microhabitat Variables

Overall, all three sites had relatively similar values for all microhabitat variables (Figure 6). The one exception to this was that Tala had much lower percent ground cover than Vato or Valo by 26% and 17% respectively. The standard deviation was the highest for percent ground cover when compared to all other microhabitat variables, ranging from 16 to 33%.

Though similar in some microhabitat characteristics, the three sites differed not only in what bamboo species were present, but how many plots actually contained bamboo. *Volohosy* bamboo stalks were only present in four plots in Tala, *volotsangana* was only present in one plot in Valo, and *tsimbolo* was found at virtually all sites.

Vato had the highest average tree DBH, percent ground cover, tree species diversity, tree abundance, average number of dead trees, and average tree height (Table 2, Figure 6). Tala had the highest average canopy cover (Table 3, Figure 6). Valo contained the highest average crown diameter and average (Table 4, Figure 6). When we combine Vato and Valo as one "minimally disturbed" site, it outcompetes Tala in average tree DBH, average crown diameter, tree species diversity, tree height (Table 5). Tala still has the highest canopy cover and tree abundance when compared to Vato/Valo as one site (Tables 3 and 5).

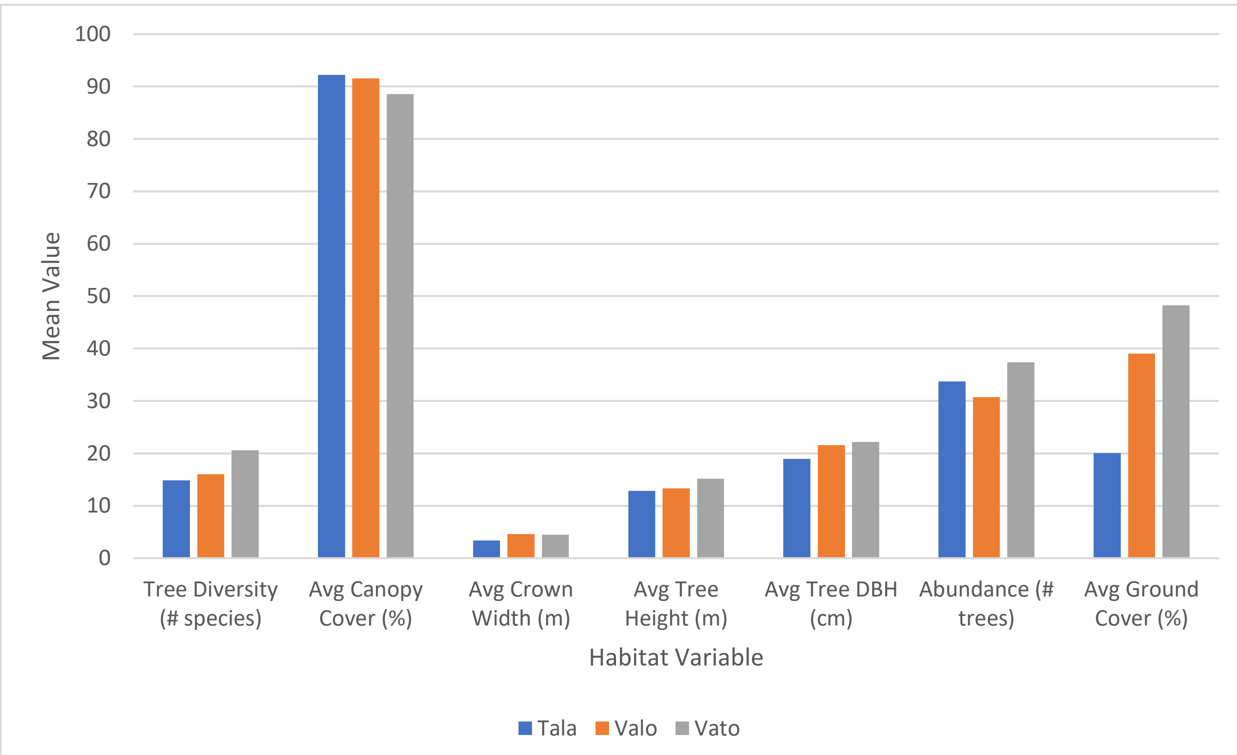


Figure 6: Forest microhabitat variables at the three study sites, Talatakely, Valohoaka, and Vatoharanana.

Table 2: Summary statistics of environmental variables in Vatoharanana, RNP.

Variable	Units	Mean	Standard Deviation	Range
Microhabitat				
tree DBH	in	8.74	0.6	8.33 – 9.68
canopy cover	%	88.6	3.1	85.4 – 93.0
ground cover	%	48.3	33.6	8.8 – 88.8
crown width	m	4.5	0.6	3.7 – 5.3
# tree species	species	20.6	4.0	17 – 27
# trees	trees	37.4	8.7	31 – 52
# dead trees	trees	3.2	2.9	0 – 8
tree height	m	15.2	1.2	13.3 – 16.3
# flowering trees	trees	2.6	0.0	1 – 4
# fruiting trees	trees	0.2	0.4	0 – 1
Volohosy bamboo	stalks	0	0	0
Volotsangana bamboo	stalks	0	0	0
Landscape				
elevation	m	1082.2	53.5	1013 – 1144
distance to main trail	m	24.1	17.6	2.5 – 38.6
distance camp/researcher building	m	638.7	183.8	125 - 872
distance to forest edge	m	1933.6	289.5	1590 – 2178

Table 3: Summary statistics of environmental variables in Talatakely, RNP.

Variable	Units	Mean	Standard Deviation	Range
Microhabitat				
tree DBH	in	7.47	1.0	6.03 – 10.07
canopy cover	%	92.2	2.0	89.3 – 95.0
ground cover	%	21.6	16.1	5 – 55
crown width	m	3.4	0.5	2.0 – 4.0
# tree species	species	14.9	3.5	9 – 21
# trees	trees	33.7	10.3	20 – 51
# dead trees	trees	2.2	2.6	0 – 8
tree height	m	12.9	1.8	10.0 – 16.0
# flowering trees	trees	1.9	3.5	0 – 13
# fruiting trees	trees	0.1	0.5	0 – 2
Volohosy bamboo	stalks	24.4	46.5	0 – 156
Volotsangana bamboo	stalks	0	0	0
Landscape				
elevation	m	947.6	43.2	861 – 1003
distance to main trail	m	32.3	21.3	5.2 – 81.6
distance camp/researcher building	m	573.3	244.0	138 – 969
distance to forest edge	m	864.6	355.2	395 – 1520

Table 4: Summary statistics of environmental variables in Valohoaka, RNP.

Variable	Units	Mean	Standard Deviation	Range
Microhabitat				
tree DBH	in	8.50	1.3	6.47 – 10.50
canopy cover	%	91.6	2.3	87.9 – 94.3
ground cover	%	39.1	22.8	8.8 – 73.8
crown width	m	4.6	0.7	3.6 – 5.7
# tree species	species	16.0	2.8	11 – 21
# trees	trees	30.8	5.6	22 – 38
# dead trees	trees	1.1	1.4	0 – 3
tree height	m	13.3	1.6	10.5 – 16.0
# flowering trees	trees	0.4	0.5	0 – 1
# fruiting trees	trees	0	0	0
Volohosy bamboo	stalks	0	0	0
Volotsangana bamboo	stalks	1.6	4.6	0 – 13
Landscape				
elevation	m	1024.9	73.0	915 – 1132
distance to main trail	m	61.4	36.6	19.7 – 137.3
distance camp/researcher building	m	471.5	272.2	325 – 808
distance to forest edge	m	1415.2	397.1	791 – 1965

Table 5: Summary statistics of environmental variables in Vatoharanana/Valohoaka (as a single site), RNP.

Variable	Units	Mean	Standard Deviation	Range
Microhabitat				
tree DBH	in	8.60	1.1	6.47 – 10.50
canopy cover	%	90.4	2.9	85.4 – 94.3
ground cover	%	42.6	26.4	8.8 – 88.8
crown width	m	4.6	0.6	3.6 – 5.7
# tree species	species	17.8	3.9	11 – 27
# trees	trees	33.3	7.4	22 – 52
# dead trees	trees	1.9	2.3	0 - 8
tree height	m	14.0	1.7	10.5 – 16.3
# flowering trees	trees	1.2	1.4	0 - 4
# fruiting trees	trees	0.1	0.3	0 – 1
Volohosy bamboo	stalks	0	0	0
Volotsangana bamboo	stalks	1.0	3.6	0 – 13
Landscape				
elevation	m	1046.9	70.0	915 – 1144
distance to main trail	m	47.1	35.2	2.5 – 137.3
distance camp/researcher building	m	536	248.3	125 – 872
distance to forest edge	m	1614.6	434.6	791 – 2178

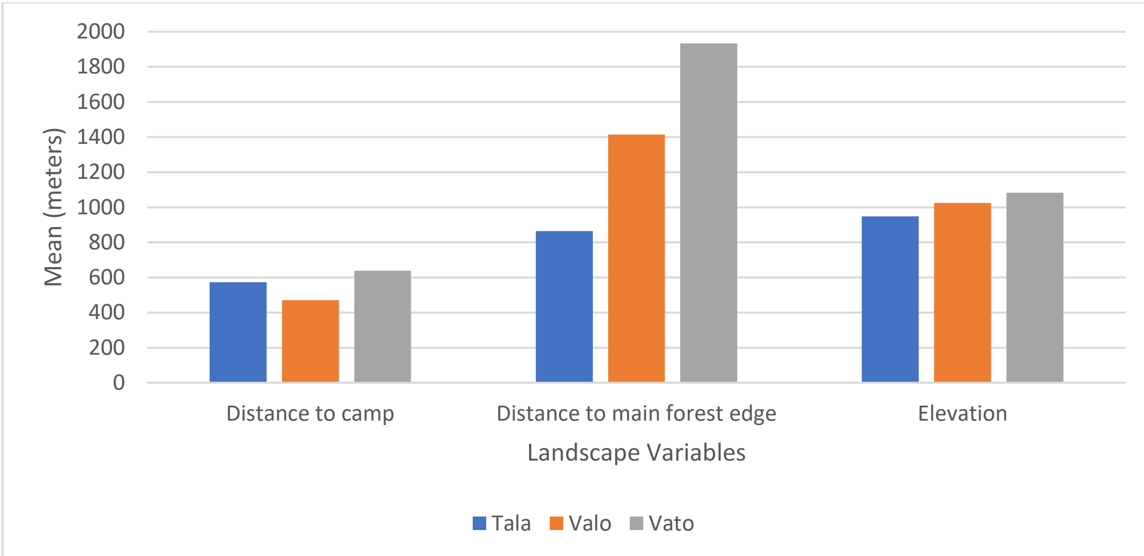


Figure 7: Forest landscape variables at the three study sites, Talatakely, Valohoaka, and Vatoharanana.

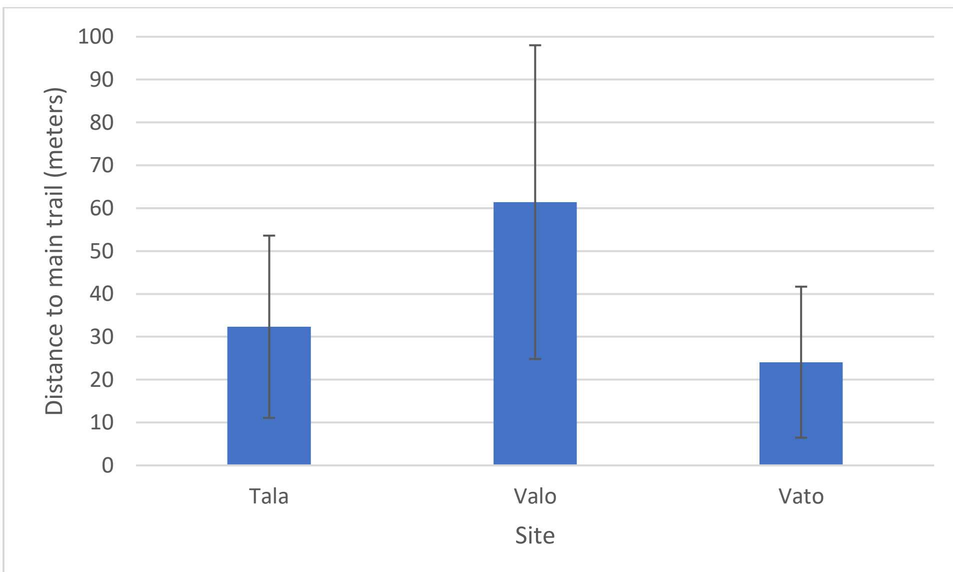


Figure 8: Average plot distances to main trail across the three study sites, Talatakely, Valohoaka, and Vatoharanana.

Landscape Variables

Vato had the highest average elevation, average distance to forest edge, and average distance to camp (Table 2, Figure 7). Valo had the highest average distance to main trail (Table 4, Figure 8). The most variability was seen in distance to forest edge, where the means of Tala and Vato differed by over 1000 meters. The only variables we realistically had control of (i.e.

how close plots were to the trail or to camp) had the least amount of variability. Distance to forest edge was mostly based on where the trail system was located.

Signs of Anthropogenic Impact

No animal traps were found in any part of Ranomafana National Park that we visited. We found one cut tree in one of our Valo plots, but we could not determine the purpose. Often bees make their hive high up in the trunk of the tree, which requires cutting the tree down to access the honey. However, the cut tree in Valo was too small to sustain a hive (18.3 cm DBH), and it was left behind for unknown reasons. Outside of our plots, we found 3 honey exploitation sites (Tables 6 and 7; Figure 9). In total, we found nine trees that were cut down, and one that was cut open but left standing. The only sign of fire we found was with the honey exploitation site on 7/20/2017.

Table 6: Description of sites where trees were cut down and exploited for honey.

Approximate Location	Date Found	Tree Species	Approximate Time Since Exploitation	Additional Notes
Between Valo & Vato	7/5/2017	• *Sandramy* *	~ 6 months	Directly across trail
Between Valo & Vato	7/11/2017	• *Rotra* • *Tavolo* • *Kalafana*	~3-4 months	Directly adjacent to trail
Talatakely	7/20/2017	• *Lambinana* ** • *Tsivalandrano* (x2) • *Tavolo* • *Tsilaitra*	~1 year old	Signs of fire were present.

* Sandramy was 56 cm DBH

** Lambinana had a large hole cut in it to extract the honey, but the tree was not cut down. The 4 smaller trees were cut down to make a walking platform up to the hive. The fire was used to drive away the bees leaving the hive empty to access the honey.

Table 7: Taxonomic description of trees cut for honey exploitation.

Malagasy Name	Family	Genus	Species
Sandramy	Anacardiaceae	*Prolorhus-Abrahamia*	*spp.*
Rotra	Myrtaceae	*Eugenia*	*spp.*
Tavolo	Lauraceae	*Cryptocarya*	*spp.*
Kalafana	Myrsinacea	*Oncostemum*	*spp.*
Lambinana	Budlejaceae	*Nuxia*	*capitata*
Tsivalandrano	Euphorbiaceae	*Drypetes*	*madagascariensis*
Tsilaitra	Oleaceae	*Noronhia*	*Spp.*

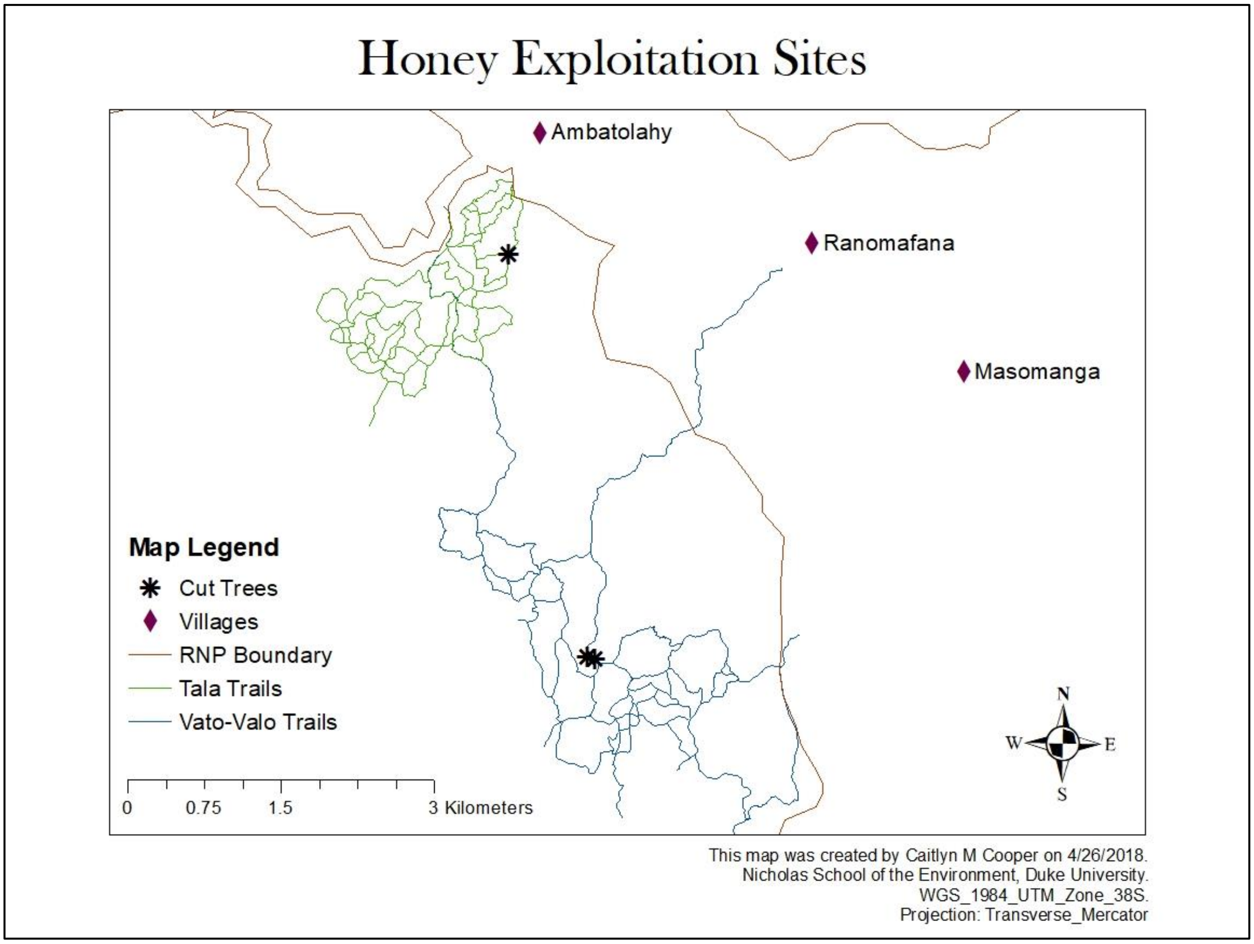


Figure 9: Honey exploitation sites found in RNP, where trees were cut down.

We incidentally found 46 zebu droppings. Out of 26 plots, we only found zebu droppings in two of our plots. One plot in Tala contained one dropping and one plot in Vato contained two droppings. All other droppings accumulated on main trails, and on ridge tops, but infrequently were off trail. Tala contained 25 total droppings, Valo contained 1 dropping, and Vato contained 20 droppings.

The only time we found trees stripped of bark was at Valo. Two student researchers did not bring rope to hang their tarps, and thus their technicians stripped bark from 2 small trees to create bark rope. Finally, we encountered two women crayfishing in Vato twice over the course of a ten-day field excursion. To the best of my knowledge, removal of any biological material from RNP without a permit is considered illegal.

Lemur Surveys

Within the plots, a total of 94 lemurs were identified during 234 plot observations. Upon removing the two sites that were directly adjacent to other plots, this totaled 77 lemurs during 216 plot observations. During incidental lemur sightings, we identified an additional 175 lemurs, totaling 269 lemurs. *Eulemur rufifrons* was the most frequently found species in study plots, totaling 27 individuals (Figure 10). The observations of *E. rufifrons* and *E. rubriventer* were sometimes repeated observations of the same group on different days, as some individuals have uniquely identifiable features to help us tell groups apart. Therefore, this does not necessarily mean that *E. rufifrons* and *E. rubriventer* were the most abundant species, but they were the most frequently observed.

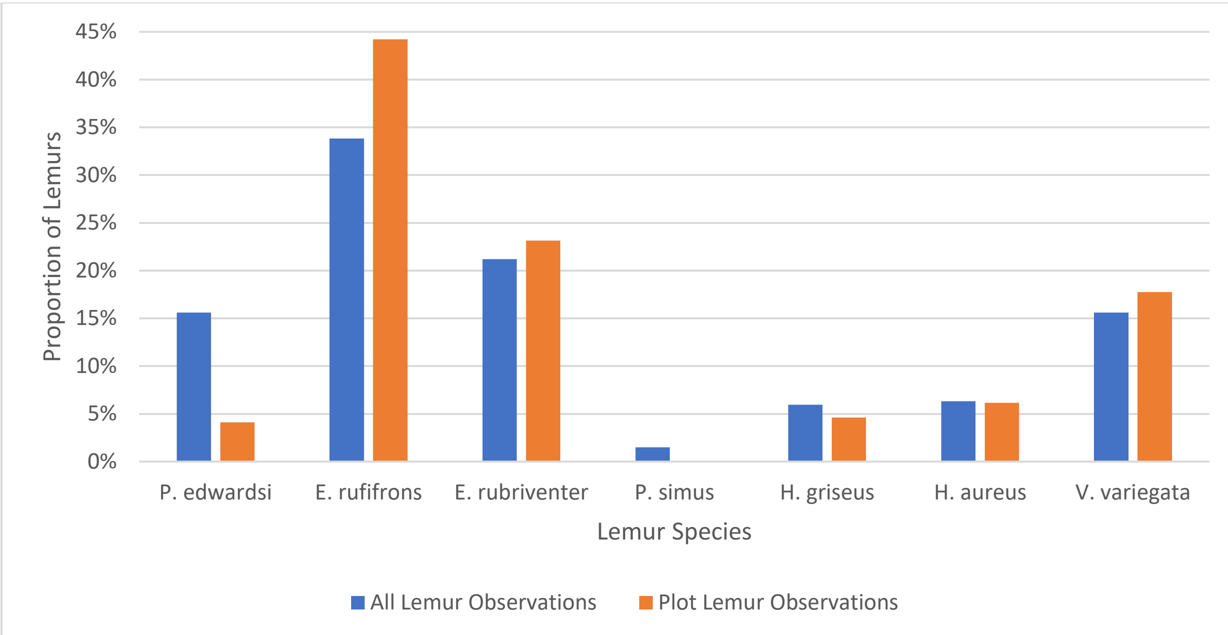


Figure 10: Bar graph shows proportion of each lemur species of all lemur observations both in and out of plots (blue) and of each species found within plots only (orange) across all sites (Talatakely, Valohoaka, Vatoharanana).

Table 8: Summary statistics on the number of lemur species (species diversity) at each site.

Site	Mean	Mode	Median	Minimum	Maximum
Tala	0.46	0	0	0	2
Vato	1.00	1	1	0	2
Valo	0.75	0	0.5	0	3
Vato/Valo	0.85	1	1	0	3

Table 9: Summary statistics on the number of lemurs (lemur abundance) at each site.

Site	Mean	Mode	Median	Minimum	Maximum
Tala	1.77	0	0	0	7
Vato	5.60	N/A	3	0	20
Valo	3.25	0	0.5	0	14
Vato/Valo	4.15	0	1	0	20

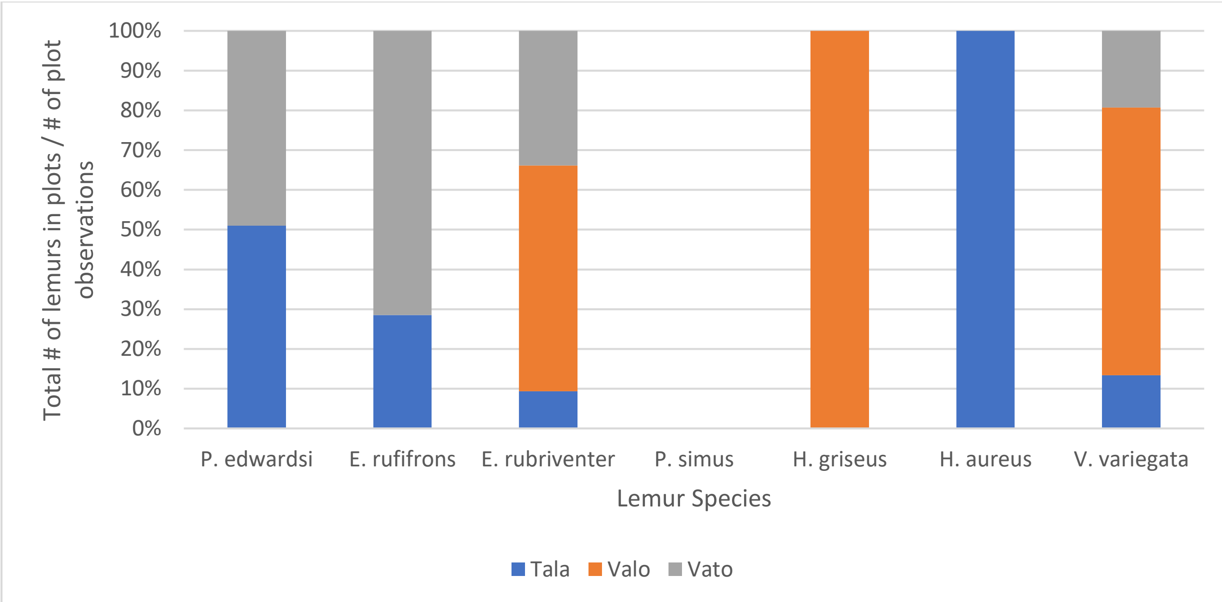


Figure 11: Bar graph shows the total number of lemurs found in research plots weighted by the total number of plot observations done at each site (Talatakely, Valohoaka, Vatoharanana).

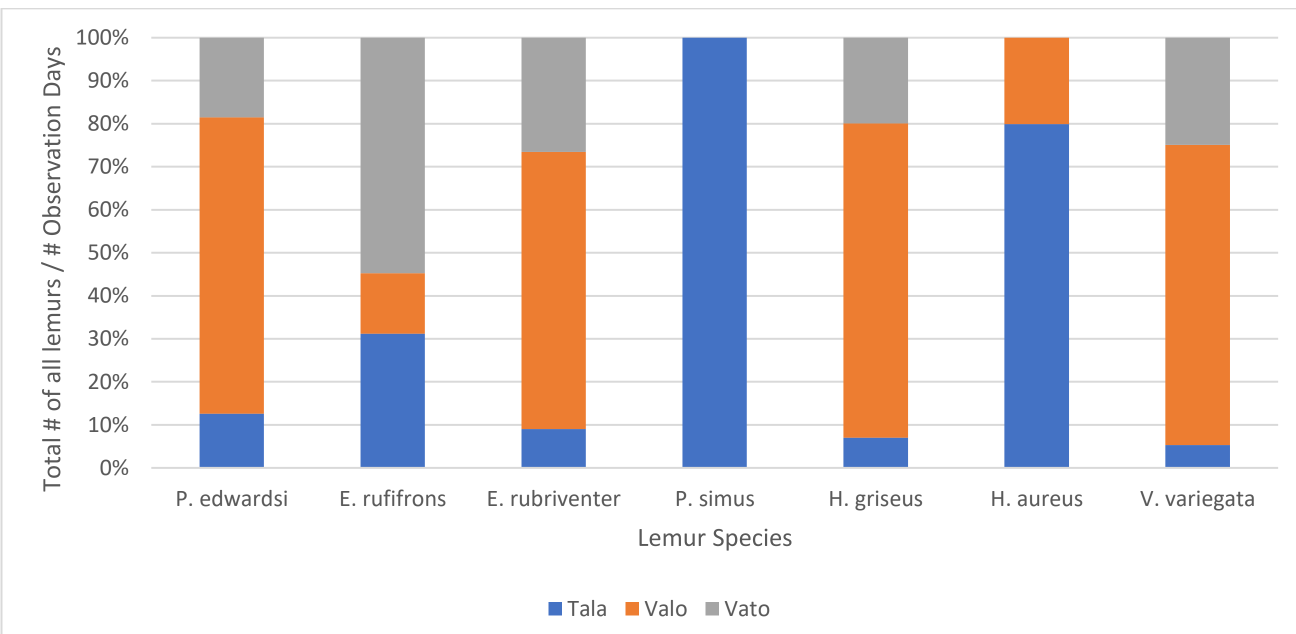


Figure 12: Bar graph shows the total number of all lemurs found in and out of plots weighted by the total number of observation days at each site (Talatakely, Valohoaka, Vatoharanana).

Table 10: Lemur species evenness (i.e. Shannon-Weiner index), abundance, and species diversity at each study site.

Site	Plot Number	Shannon Weiner Index	Lemur Abundance	Lemur Species Diversity
Tala	58	0	0	0
	101	0	1	1
	103	0.69	6	2
	105	0	0	0
	106	0	0	0
	107	0	0	0
	108	0	3	1
	109	0	0	0
	110	0	6	1
	111	0	0	0
	112	0	7	1
	113	0	0	0
	114	0	0	0
Valo	201	0	4	1
	202	0	0	0
	203	0	1	1
	204	0.96	14	3
	205	0	0	0
	206	0	7	1
	207	0	0	0
	208	0	0	0
Vato	301	0	4	1
	302	0.64	3	2
	303	0	1	1
	304	0	20	1
	305	0	0	0

When looking only at plot observations, *H. griseus* appears to only be found in Valo (Figure 11). However, when looking at all plot and incidental observations combined, we find that *H. griseus* is actually present at all three sites (Figure 12). Similarly, plot observations show *H. aureus* was only found in Tala, but incidental observations show it is present in Valo as well

(Figures 11 and 12). The remaining two individuals of *P. simus* were only found in Tala but were not found in any of the plots. Proportions of *V. variegata* and *E. rubriventer* were similar both inside and outside of research plots.

Vato had the highest mean lemur diversity and mean lemur abundance per plot, followed by Valo, then Tala (Tables 8-10). One plot at Valo had the highest recorded Shannon-Weiner diversity index (0.96), followed by a plot at Tala (0.69), and a plot at Vato (0.64) (Table 10). Shannon-Weiner diversity index values could only be calculated for plots that contained more than one lemur species, whereas only one species type was observed at most plots.

Data Analysis - Mantel's Tests

When evaluating large matrices of habitat variables, we did not find any significance with lemur species composition or presence/absence when holding all other variables constant (Table 11 and 12). However, we did find that landscape variables as a group were significantly related to geography (p-value 0.03995), when not holding any other variables constant.

When looking at both species composition and presence-absence, we found significant relationships with two species: *H. aureus* and *V. variegata* (Tables 13-15). We also found significant relationships with *E. rubriventer* for presence-absence data only (Tables 14 and 15). Since *P. simus* was not found at any plots, we could not include this species in our analysis.

Table 11: Results of large matrix Mantel tests between lemur species composition and groupings of landscape, microhabitat, and geographic variables. NS indicates not significant. Table is read from left to right such as "Lemur species composition is not significantly related to microhabitat variables when holding landscape and geographic variables constant."

	Lemur Species Composition	Microhabitat Variables	Landscape Variables	Geographic Variables
Lemur Species Composition		NS	NS	NS
Microhabitat Variables	NS		NS	NS
Landscape Variables	NS	NS		NS
Geographic Variables	NS	NS	NS	

Table 12: Results of large matrix Mantel tests between lemur species presence/absence and groupings of landscape, microhabitat, and geographic variables. NS indicates not significant. Table is read from left to right such as "Lemur species presence/absence is not significantly related to microhabitat variables when holding landscape and geographic variables constant."

	Lemur Species Presence/Absence	Microhabitat Variables	Landscape Variables	Geographic Variables
Lemur Species Presence/Absence		NS	NS	NS
Microhabitat Variables	NS		NS	NS
Landscape Variables	NS	NS		NS
Geographic Variables	NS	NS	NS	

Table 13: Landscape, microhabitat, and geographic variables significantly (at $P \leq 0.05$) related to lemur species composition as determined by partial Mantel tests; partial Mantel correlations are seen in parentheses.

Lemur Species	**Variable**	**Variables held constant**
Hapalemur aureus	# of bamboo stalks (0.3478)	All other microhabitat variables
Varecia variegata	Average tree DBH (0.4795)	All other microhabitat variables
Varecia variegata	Average tree DBH (0.3809)	All microhabitat, landscape, and geography variables constant
Varecia variegata	Latitude (0.2940)	Longitude

Table 14: Landscape, microhabitat, and geographic variables significantly (at $P \leq 0.05$) related to lemur species presence/absence as determined by partial Mantel tests; partial Mantel correlations are seen in parentheses.

Lemur Species	Variable	Variables held constant
Hapalemur aureus	# of bamboo stalks (0.3478)	All other microhabitat variables
Eulemur rubriventer	Distance to camp (0.2241)	All microhabitat, landscape, and geography variables constant
Varecia variegata	Average canopy cover (0.1894)	All other microhabitat variables
Varecia variegata	Average canopy cover (0.1830)	All microhabitat, landscape, and geography variables constant
Varecia variegata	Average tree DBH (0.2906)	All other landscape variables
Varecia variegata	Average tree DBH (0.2282)	All microhabitat, landscape, and geography variables constant
Varecia variegata	Tree density (0.1997)	All other microhabitat variables
Varecia variegata	Tree density (0.1963)	All microhabitat, landscape, and geography variables constant

Table 15: Landscape, microhabitat, and geographic variables significantly related to lemur species composition or presence/absence as determined by partial Mantel tests. Relationship of variables in parentheses.

Lemur Species	Species Composition	Presence/Absence
Propithecus edwardsi	NS	NS
Eulemur rufifrons	NS	NS
Eulemur rubriventer	NS	Distance to camp (-)
Hapalemur griseus	NS	NS
Hapalmeur aureus	# of bamboo stalks (+)	# of bamboo stalks (+)
Varecia variegata	Average tree DBH (+)	Average tree DBH (+) Average canopy cover (+) Tree density (-)

Data Analysis - ANOVA

I compared the three sites individually including Tala (heavily logged), Vato (selectively logged), and Valo (pristine forest) using ANOVA. Tree diversity, canopy cover, crown width, tree height, DBH, ground cover, and tree density met the assumption of normality. Dead trees, flowering and fruiting trees were non-normal; therefore, those variables were analyzed with the non-parametric Kruskal-Wallis test.

The null hypothesis of ANOVA is that the population means are the same between the sites. We failed to reject the null hypothesis for four microhabitat variables between Tala and Vato, one variable between Tala and Valo, but no variables between Vato and Valo (Table 16). When running the Kruskal-Wallis test, the only significance was on flowering trees (Table 16), but this cannot be distinguished between sites since we cannot run Tukey Post-Hoc Test on a Kruskal-Wallis test.

Tree DBH was significant (p-value: 0.0311) when running ANOVA, but only slightly significant when running Tukey Post-Hoc Test (adjusted p-value: 0.08008 between Valo and Tala; adjusted p-value 0.06734 between Vato and Tala). There was no significance for tree density, number of dead trees, average ground cover, or fruiting trees.

For our landscape analysis, distance to cultivated patch, distance to forest edge, distance to camp, and elevation met the assumptions of normality. Distance to trail and zebu poop were non-normal; therefore, those variables were analyzed with the non-parametric Kruskal-Wallis test. We failed to reject the null hypothesis for two landscape variables between Tala and Vato, three variables between Tala and Valo, and none between Vato and Valo (Table 16). There was no significance for distance to camp or research site, distance to trail, or zebu poop.

When analyzing lemur abundance, lemur diversity, and each individual lemur species, none of the variables met the assumption of normality. The results of the Kruskal-Wallis tests found no significance for any lemur variables (Table 16)

Table 16: Results from ANOVA and Kruskal-Wallis tests for microhabitat and landscape variables between sites. Adjusted p-values are in parentheses.

	Tala vs. Vato	Tala vs. Valo	Vato vs. Valo	General
Microhabitat Variables	• Crown width (0.00688) • Canopy cover (0.01938) • Tree diversity (0.01173) • Tree height (0.03603)	• Crown width (0.00046)	NS	• Flowering trees (0.02162) • Tree DBH (0.0311)
Landscape Variables	• Distance to forest edge (0.00005) • Elevation (0.00026)	• Distance to forest edge (0.00957) • Distance to cultivated patch (0.01346) • Elevation (0.00937)	NS	NS
Lemur Variables	NS	NS	NS	NS

Table 17: Results from T-tests and Wilcoxon-Mann-Whitney tests for microhabitat and landscape variables between sites. P-values are in parentheses.

	Tala vs. Vato/Valo
Microhabitat Variables	• Crown width (p-value = 4.074e-05) • Tree DBH (p-value = 0.00840) • Ground cover (0.03525)
Landscape Variables	• Distance to cultivated patch (0.00251) • Distance to forest edge (0.00011) • Elevation (0.00014)
Lemur Variables	NS

Data Analysis - T-Tests

I compared the habitat and lemur variables of Tala to Vato/Valo as a single site using a two-tailed t-test. When checking the data for equal variance, all microhabitat variables had equal variance except for fruiting and flowering trees. For landscape variables, only zebu poop did not meet the assumption of equal variance. When checking the data for normality, ground cover, dead trees, flowering trees, fruiting trees, distance to trail, and zebu poop were non-normal, and thus were analyzed with the non-parametric Wilcoxon-Mann-Whitney test. All other microhabitat and landscape variables were normally distributed, and thus analyzed with the parametric t-test.

The null hypothesis of the t-test is also that the population means are the same between the sites. We reject the null hypothesis for three microhabitat variables and three landscape variables (Table 17). However, we did not find significance for tree diversity, canopy cover, tree height, tree density, or distance to nearest camp or research station.

Results from the Wilcoxon-Mann-Whitney tests yielded significance only for ground cover, but did not find significance for dead trees, flowering trees, fruiting trees, distance to main trail or zebu poop. Therefore, we can reject the null hypothesis that the distributions of both populations are equal regarding ground cover.

When analyzing lemur abundance, lemur diversity, and each individual lemur species, again, none of the variables met the assumption of normality. The results of the Kruskal-Wallis tests also found no significance for any lemur variables between Tala and Vato/Valo (Table 17).

Data Analysis – Pearson Product-Moment Correlation

When looking at correlations between habitat variables, the highest were between tree DBH and crown diameter (0.79), distance to cultivated patch and main forest edge (0.88), distance to cultivated patch and elevation (0.74), and latitude and longitude (0.86) (Tables 19 and 20). Several landscape variables were strongly correlated with longitude (Table 20), including latitude, distance to forest patch edge, distance to main forest edge, and elevation.

GPS Accuracy

The error when using the Trimble Juno 3B ranged from 8 to 23 meters and averaged 11.5 meters. The PDOP (Precision Dilution of Position) ranged from 1.4 to 5.77 and averaged 2.58. Our satellite coverage ranged from 4 of 4 satellites to as high as 10 of 11 satellites. On average we maintained 6 of 7 satellites. Accuracy was somewhat limited in our GPS measurements as real-time correction and post-processing was not available since there is not a CORS station near the study site.

Discussion

Microhabitat

Overall, there were several similarities in the microhabitat of RNP to what has been found in previous studies. We found that tree height was significantly taller in Vato than in Tala, which is consistent with past studies (Balko & Underwood 2005; Tecot 2008; Herrera et al. 2011). Tree DBH was also higher in Vato than Tala, but only slightly approached significance, which is consistent with Tecot's findings (Tecot 2008). Balko and Underwood also found a higher tree DBH in Vato, however in their study the difference was statistically significant (Balko & Underwood 2005).

Some results show that new changes have emerged. Over the past 12 to 14 years, the tree DBH between Tala and Vato has become more similar, while tree height has become more different. Tecot (2008) reported that trees in Tala were "on average 37% smaller and 11% (Balko and Underwood, 2005) to 12% (this study) shorter" than in Vato. In comparison, the results of this study show that trees in Tala are only 14.5% smaller, but 15.1% shorter. We found that crown width was higher in Vato/Valo than in Tala, which was statistically significantly different between sites. However, Tecot (2008) previously found crown diameter was higher in Tala than in Vato, but not statistically significant. Balko and Underwood (2005) found that canopy cover was approximately the same across sites, and Herrera et al (2016) found that canopy cover was significantly higher in Vato than Tala. However, our results show that canopy cover is now significantly higher in Tala than in Vato.

To answer our research questions 1a and 1b, "Is there a significant difference in microhabitat characteristics between sites," we did find a significant difference between Tala and Vato for tree diversity, canopy cover, crown width, and tree height. In contrast, Tala and Valo only showed a significant difference for crown width. No significant differences were found between Vato and Valo specifically.

Since Tala and Valo are the most different in terms of historical disturbance, we expected to find the most microhabitat differences between these locations. It was also surprising to see that Vato and Valo had no significant differences between them. Though they are considered separate locations, this result may be due to the fact that it is hard to tell the exact boundary between Vato and Valo (Appendix, Figure 13). Therefore, Vato and Valo likely share more similarities than differences. However, it is clear that these three sites provide unique habitat characteristics for different species.

Landscape Analysis

We found that elevation did not differ much across the three sites. However, this was based on a Digital Elevation Model (DEM). Had we measured elevation at each plot, we likely would have found more variation. Vato plots were located the furthest from the forest edge, and Tala plots were the closest to the forest edge, which is easily explained by the nature of where the trail system is placed (Figures 3 and 13). Though elevation and distance to forest edge differed between plots, no lemur species showed any significant relationships to these landscape variables.

All research plots appeared to be relatively similar distances from camp or research buildings, with Valo plots being the closest, and Vato plots being the furthest. Therefore, our study design was successful in distributing research plots around and away from camp. There was a lot of variation in plot distance to main trail, which was expected since we purposely chose plots at a variety of distances from the trail.

To answer our research questions 2a and 2b, "Is there a significant difference in landscape characteristics between sites," we did find a significant difference between Tala and Vato for distance to forest edge and elevation. We found the same differences between Tala and Valo, but also found a significant difference in the distance to cultivated patch. Again, no significant differences were found between Vato and Valo specifically.

Signs of Anthropogenic Impact

We found only some signs of anthropogenic impact in RNP. We did not find any animal traps, which is expected, since hunting or capturing of lemurs is rarely seen in this area (Wright et al. 2012). However, since RNP is a protected area, we did not expect to find trees exploited for honey. We found three honey exploitation sites which resulted in a total of nine cut trees. Among these were several tree species that are known food sources for lemurs (Overdorff 1993; White et al. 1995)

The locations of these exploitation sites hint that the trespassers likely came from Ranomafana. The entrance to RNP and Talatakely are frequented by guides and tourists making it less likely for crimes to occur in these areas. However, Vato and Valo are less frequently visited, and therefore less supervised. Two of the exploitation sites were found not far from the trail that leads directly to Ranomafana (Figure 9). The third exploitation site was found far off trail on the eastern side of Talatakely, closer to Ranomafana (Figure 9). This part of Talatakely is not as frequented by tourists since it is on a steep hill with no stairs. The exploitation events were not recent, making it difficult to estimate when the crime occurred. We were not able to make any conclusions about the relationship between cut trees and lemur species since so few cut trees were found.

The presence of zebu livestock is considered an anthropogenic impact since the zebu are free to roam the forest and browse. However, a consequence of this is an increased quantity of zebu feces in the forest. It is important to note the frequency or location of zebu droppings because 1) lemurs sometimes participate in coprophagy [3] and 2) fecal matter often contains

[3] the consumption of fecal matter

transmittable diseases (Loudon et al. 2006; Fish et al. 2007). The presence of zebu feces was highly localized on trails and ridgetops. It was rarely found off-trail which shows that its impact is not widespread. It was not significantly different between research sites, nor was it significantly related to any lemur species. This implies that at this time it is not having any measurable effect on lemur presence or abundance.

As researchers, we cannot ignore the fact that we too can have an impact on the environment. Some small, live trees were cut or stripped of bark for setting up camp. Only deadwood was supposed to be used for making camp fires. However, by removing deadwood we are changing the microhabitat. Deadwood is a valuable carbon sink, and is also important for fungi, bacteria, insects, and nesting species (Dudley & Vallauri 2005; Pfeifer et al. 2015). Other sites that are more popular with researchers end up using all available deadwood resulting in cutting live trees for camp fire meals. Realistically, this is not a sustainable practice, and is not benefiting the park environment. Alternative forms of fuel, or more efficient uses of fuel, should be considered for future projects.

Lemur Surveys

Our research comparing lemurs and their habitat found two previously cited relationships, and several new ones. First, we found that *V. variegata* were positively, significantly related to canopy cover which was also found by Herrera (Herrera et al. 2011). It should be noted that our methods for measuring canopy cover differed from Herrera's. We used a densiometer for an in-depth assessment, while Herrera's study used a rapid estimation method of canopy closure. Yet, both methods resulted in the same significant result.

V. variegata were also significantly related to tree DBH and tree density. A simple correlation showed that *V. variegata* were negatively related to tree density, but positively related to tree DBH. Larger DBH trees are more likely to be mature enough to produce fruit, *V. variegata*'s primary food source. *V. variegata* have also been previously recorded showing preference for foraging in large DBH trees (Balko and Underwood 2005). The negative relationship with tree density is likely due to tree crowding, leading to decreased sun exposure to food trees, and thus a lower production of fruit, as hypothesized by Balko and Underwood (2005).

A new pattern emerged where we found *V. variegata* in Tala, where they have not previously shown any interest in foraging (Herrera et al 2011, Wright et al 2012). Wright et al (2012) states that "The strictest frugivore, *V variegata*, did not occur in the high disturbance level site (Talatakely) where the big canopied fruit trees were removed (Balko and Underwood 2005)." Tala has now recovered to a point of having larger canopy cover, but still has a smaller average canopy width than Vato and Valo. It is possible that *V. variegata* are actually drawn to the invasive Chinese guava in Tala as opposed to other fruiting trees, which would explain why we did not find a significant relationship between this species and fruiting trees. However, in this study, *V. variegata* were most frequently found in fruiting *rotra* (*Eugenia spp*, Myrtaceae family), and fruiting *sandramy* (*Prolorhus-Abrahamia spp*., Anacardiaceae family) trees (personal observation). Therefore, more research needs to be done to fully understand which habitat factors are enticing *V. variegata* to begin foraging in Tala for the first time in decades.

The only lemur species that were significantly related to differences in microhabitat or landscape variables were *Hapalemur aureus, Eulemur rubriventer*, and *Varecia variegata*. All three of these species diets are highly specialized. *H. aureus's* diet is 88% bamboo, 78% of which is a single bamboo species (*volosy*) (Tan 1999). *E. rubriventer* spends 75% of its time feeding on fruit (Tecot 2008), and *V. variegata's* diet is 70.8% fruits (White et al. 1995).

Prolemur simus also has a highly specialized diet (95% bamboo) (Tan 1999), but we did not identify this species in our plots, and thus were unable to analyze its relationship with different habitat variables. Among the three bamboo lemurs, *Hapalemur griseus* is the least specialized, whose diet consist of 72% *volosy* bamboo. *H. griseus* also feeds on more plant species than the other two bamboo lemurs, showing it has more flexibility in its diet. Of the remaining diurnal lemurs in RNP, *Propithecus edwardsi* consume equal proportions of leaves, fruit, and seeds (Hemingway 1998 in Wright 2012) and *Eulemur rufifrons* diet is 66.8% fruit (Overdorff 1993).

To answer research questions 1 and 2, "What is the relationship between lemur species composition/abundance and habitat at the *landscape* and *microhabitat* scales in RNP?" we found that specialist lemur species are the drivers of lemur community composition differences. This is especially prevalent at the microhabitat scale, as multiple microhabitat factors were significant, whereas only one landscape variable was significant.

To answer research question 3, "What is the relative strength of the relationships between lemur species composition/abundance and habitat at two spatial scales?" we ultimately need more data. Despite our attempt to avoid issues of spatial autocorrelation, some spatial relationships were still present. *V. variegata* were significantly related to latitude, and several landscape variables were strongly correlated (and significantly related) to geography. The strongest relationship we found was between *H. aureus* and bamboo abundance (partial mantel correlation: 0.3478), which is to be expected since bamboo is the primary source of their diet.

Finally, to answer research question 4, “Is there a significant difference in lemur species composition/abundance between Tala, Vato, and Valo?” – no, we did not find a difference in lemurs between sites. It is possible both previously disturbed sites have recovered to a point of sustaining populations of all species, even if they have not recovered fully. Differences are still present between these sites, but they likely are not heavily influencing lemur presence or abundance.

Assessment of Point Plot Methodology for Lemurs

When implementing random point plot methods for lemur surveys, we found that we had relatively low detection rates making it difficult to reach a species saturation curve (Figure 15). Ideally we would have continued to survey until a species saturation curve had been met to show that all possible species have been sampled, and no new species were likely to be found. However, since lemurs are territorial of their habitat area and will fight to defend their food source, we rarely found more than one species within the 20 meter by 20 meter plots (Rendigs et al. 2003; Wright et al. 2012). We often saw the same group of lemurs at the same plot multiple times. A longer sampling time period, and many more plot surveys, would be necessary to reach a species saturation curve.

When comparing the lemur sightings in plots to all lemur sightings, it appeared that the plots were not entirely representative of lemur composition throughout the area (Figures 11 and 12). Plot observations appeared to overestimate *E. rufifrons*, and underestimate *P. edwardsi* and *P. simus* abundance. This might partially explain why we did not find any significant habitat relationships with these three species. However, lemur observations in plots appeared to be representative of the population for *E. rubriventer, H. griseus, H. aureus,* and *V. variegata* (Figure 10). This resulted in finding significance for three of those species. Overall, the plot method works to find significant relationships, but could be greatly improved with a higher sample size, greater sampling effort, and longer sampling period. Even with these improvements, point plots, among other methods, would likely still miss rare species like *P. simus*. To study the relationship between *P. simus* and their habitat, one would have to follow the remaining pair and study the different microhabitats that they visit.

Increasing the plot size or observation area around the plot would also increase the chances of finding more than one species in the area. However, the observation area realistically should not stray far from the plot, as the microhabitat can change rather quickly. If lemurs were observed too far from the plot, it would be difficult to be able to make any conclusions about the relationship between them and their habitat. Increasing the plot size would increase the time it takes to sample the microhabitat. Though, other studies have also used 20 by 20 meter plots (400 m^2), and some have reported using larger plots of 500 m^2 (Ralison et al. 2015; Johnson & Overdorff 1999).

Limitations

One of the limitations in this study is understanding the historical boundary between Vato and Valo. The exact mapping of where the logging occurred seems to have been lost over time. It would be quite beneficial for Vato and Valo to be re-mapped designating where the pristine forest ends, and historically altered habitat begins.

Second, due to difficult terrain and time constraints, we were limited to studying areas within RNP where trails were already present. Though it is possible to create new transects by cutting vegetation, for the goals of this study I did not want to alter the microhabitat. Therefore, the plots were always by some degree within walking distance of a trail. Third, by studying one park and creating multiple plots withing the same habitat area, apsects of this study were pseudo-replicated. Ideally, a larger study would apply this methodology to multiple parks or protected areas.

Conclusions

The results of this study show that the microhabitat and landscape characteristics between Tala, Vato, and Valo are significantly different from each other. Some habitat factors have stayed the same since past studies over a decade ago, while some habitat factors have begun to shift. As succession continues post-disturbance, it is possible more similarities between these locations will arise as the ecosystem equilibrates. Despite these habitat differences, lemur abundance and composition do not significantly differ between sites. It is most likely that the habitat factors that most influence their presence or abundance do not differ between sites.

Three of the seven diurnal lemur species in RNP showed significant relationships with different habitat factors, which appeared to be driven by their specialized diets. The one exception is the negative relationship between *E. rubriventer* and distance to camp or research building. At this time we do not have enough evidence to make any assumptions about why this negative relationship occurs. But it is clear that some aspect of anthropogenic presence is driving *E. rubriventer* further from human-occupied areas. Finally, anthropogenic activity such as cutting trees, crayfishing, and zebu cattle browsing are still present in the park. Though this activity is occurring at such low levels that any potential negative effects from them are negligable.

Future Directions

Future studies would benefit from expanding upon this study by including new research areas throughout RNP, increasing the sample size, sampling effort, and potentially increasing the plot observation area. Essentially, when done on a larger scale, more coclusions could be made about the relationship between lemurs and their environment.. Also, this study could be conducted in other forested areas to see if the same species located in different environments have the same habitat requirements. This would allow us to ask questions like “Do all *V. variegata* require certain canopy cover requirements to occupy an area? Is canopy cover and essential requirement to maintain a *V. variegata* population?” Once the study is repeated in multiple areas, creating a larger sample size, we would be able to apply the results regionally instead of just locally.

The habitat factors I explored are not an exhaustive list. Recording additional habitat characteristics could uncover new relationships. Additional landscape analysis could include distance to nearest water source such as a river or creek. It could also be beneficial to record ancillary data such as temperature, precipitation, air quality, etc. Air quality is especially important to consider during times of tavy, or burning of land for crops, where smoke sweeps across the land. Often ancillary data can explain abnormalities in the data such as on days of heavy rains or extreme heat. Finally, it would be important to conduct the same study on nocturnal species, since so few studies prioritize nocturnal lemurs over diurnal ones.

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Appendix I

Definitions

1. Signs of anthropogenic/human presence

    a. Lemur traps (or any animal trap)

    b. Cattle dung

    c. Cut trees

    d. Cut branches

    e. Machete cuts

    f. Signs of fire

    g. Trees exploited for honey

    h. Presence of humans not part of research team

    i. Stripped bark

Table 18: All Lemur Species Found in RNP

Latin Name	Common Name	Home Range (hectares)	Status
Avahi peyrierasi	Peyrierasi's woolly lemur	1 (IUCN)	VU
Cheirogaleus sp.	Not yet described (Dwarf Lemur)	Not yet known	DD
Daubentonia madagascariensis	Aye-aye	31-214 (Sterling 1993)	EN
Eulemur rufifrons	Red-fronted lemur	100-300 (Tan 1999)	NT
Eulemur rubriventer	Red-bellied lemur	19-40 (Tan 1999)	VU
Hapalemur aureus	Golden bamboo lemur	26 (Tan 1999)	CR
Hapalemur griseus	Gray gentle bamboo lemur	15- 20 (IUCN, Tan 1999)	VU
Lepilemur microdon	Small toothed sportive lemur	0.5 – 1.5 (Porter 1998)	EN
Microcebus rufus	Brown mouse lemur/ Rufous mouse lemur	Not yet known (Atsalis 2000)	VU
Prolemur simus	Greater bamboo lemur	40-62 (IUCN, Tan 1999)	CR
Propithecus edwardsi	Milne Edward's sifaka	100-250 (Tan 1999)	EN
Varecia variegata editorium	Black and white ruffed lemur/ Southern ruffed lemur	127 (IUCN)	CR

*NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, DD = data deficient. Status based on IUCN 2014 assessment.

Annotated Bibliography on Anthropogenic Impacts on Lemurs

Lehman, S.M., Rajaonson, A. & Day, S., 2006a. Edge effects and their influence on lemur density and distribution in southeast Madagascar. *American Journal of Physical Anthropology*, 129(2), pp.232–241.

- Lehman et al found that some lemurs are either positively affected or not affected by forest edges in Vohibola III Classified Forest. This included two diurnal species, *Hapalemur griseus griseus* (Eastern lesser bamboo lemur), and *Eulemur rubriventer* (red-bellied lemur), and two nocturnal species, *Microcebus rufus* (Rufous mouse lemur), and *Avahi laniger* (Eastern wooly lemur). The authors state that more data are needed on how forest edges affect lemurs in other areas of Madagascar.

Lehman, S.M., Rajaonson, A. & Day, S., 2006b. Edge effects on the density of *Cheirogaleus major*. *International Journal of Primatology*, 27(6), pp.1569–1588.

- Lehman et al also found that *Cheirogaleus major* (the greater dwarf lemur) is negatively affected by forest edges in Vohibola III Classified Forest. The results showed that the greatest dwarf lemur densities were found 700-1250 meters from the forest edge. They also found that *Cheirogaleus major* correlated with tree DBH since larger DBH trees produced the fruit in *Cheirogaleus major*'s diet.

Bublitz, D.C. et al., 2015. Pathogenic enterobacteria in lemurs associated with anthropogenic disturbance. *American Journal of Primatology*, 77(3), pp.330–337.

- With increasing habitat overlap between lemurs and humans, there is an increase of contact between the two. This increases lemurs exposures to new pathogens. Bublitz et al compared lemurs in an intact forest to those in a degraded forest in Ranomafana National Park. The results found that only lemurs in the degraded habitat tested positive for

pathogens, and they were the same pathogens that were found in human, cattle, and rodent fecal samples as well. Therefore, lemurs in more anthropogenically disturbed sites were at a greater risk for infection.

Dunham, A.E. et al., 2008. Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur. *Biological Conservation*, 141(1), pp.287–297.

- Dunham et al used population modeling to see how deforestation, hunting, and El Niño events affected lemur populations. Authors noted that habitat decline was mostly caused by slash and burn agriculture. Model results showed that deforestation and hunting, even at conservative levels, would result in considerable lemur population declines. Modeling El Nino events found that they decrease lemur fecundity. Authors note more data is needed on “relation between habitat quality and its effect on viatal rates for each subpopulation.”

Ganzhorn, J.U., 1995. Low-level forest disturbance effects on primary production , leaf chemistry , and lemur populations. *Ecology*, 76(7), pp.2084–2096.

- Ganzhorn looked at low-intensity logging in western Madagascar and found that logging exposed trees to more sunlight which resulted in a higher protein content. Therefore the leaves had a higher leaf quality, which would be beneficial for folivores. Ganzhorn also found that fruit production increased, which would be beneficial for frugivores. Overall, Ganzhorn found more lemurs of all species in the low-intensity logged areas than in the pre-logged state, but found a decline in lemurs in high-intensity logging areas.

Herrera, J.P. et al., 2011. The effects of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. *International Journal of Primatology*, 32(5), pp.1091–1108.

- Herrera et al surveyed a heavily logged forest and a lightly diturbed forest using

circuitous survey routes on pre-existing trails where possible in Ranomafana National Park. They found that *Avahi peyierasi* abundance was higher in the lightly disturbed forest, whereas *Microcebus rufus* abundance was higher in the heavily logged forest. *Varecia variegata* were only found in the lightly disturbed forest. *Eulemur rubriventer* was found in similar abundances at both sites.

Additional Figures and Tables

Table 19: Pearson product moment correlations among microhabitat features. Correlations above 0.5 are highlighted.

Variable	# tree species	canopy cover	crown diameter	tree height	DBH	# trees	# dead trees	ground cover	bamboo stalks	flowering trees	fruiting trees
# tree species	1.0	0.52	0.31	0.48	0.25	0.62	0.41	0.52	0.29	0.17	-
canopy cover		1.0	0.22	0.15	0.17	0.41	0.36	0.59	0.13	0.12	-
crown diameter			1.0	0.64	0.79	0.26	0.32	0.35	0.63	0.12	0.16
tree height				1.0	0.54	0.14	0.18	0.13	0.37	0.35	0.18
DBH					1.0	0.42	0.21	0.27	0.52	-	0.096
# trees						1.0	0.43	0.093	0.23	0.25	-
# dead trees							1.0	0.27	0.37	0.19	0.13
ground cover								1.0	0.34	0.17	0.26
bamboo stalks									1.0	0.22	0.11
flowering trees										1.0	0.13
fruiting trees											1.0

Table 20: Pearson product moment correlations among landscape and geographic features. Correlations above 0.5 are highlighted.

Variable	Zebu poop	Cut trees	Distance to main trail	Distance to camp	Distance to main forest edge	Distance to forest patch edge	Elevation	Latitude	Longitude
Zebu poop	1.0	0.055	0.16	0.22	0.20	0.15	0.34	-	0.12
Cut trees		1.0	-	0.19	0.17	0.15	0.21	0.37	0.22
Distance to main trail			1.0	0.30	0.16	0.40	0.19	0.22	0.27
Distance to camp				1.0	0.40	0.52	0.19	0.064	0.15
Distance to main forest edge					1.0	0.88	0.82	0.20	0.63
Distance to forest patch edge						1.0	0.74	0.18	0.62
Elevation							1.0	0.32	0.67
Latitude								1.0	0.86
Longitude									1.0

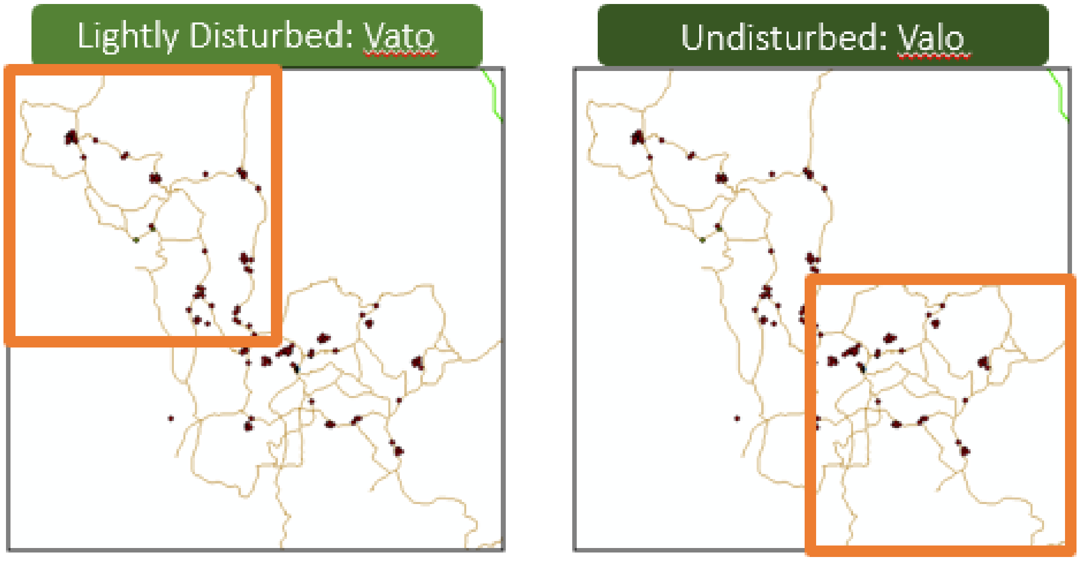

Figure 13: The boundary between Vato and Valo is indistinct. Though, for the purposes of this study, Vato was the northwestern most part of the trail system, and Valo was the southeastern most part of the trail system.

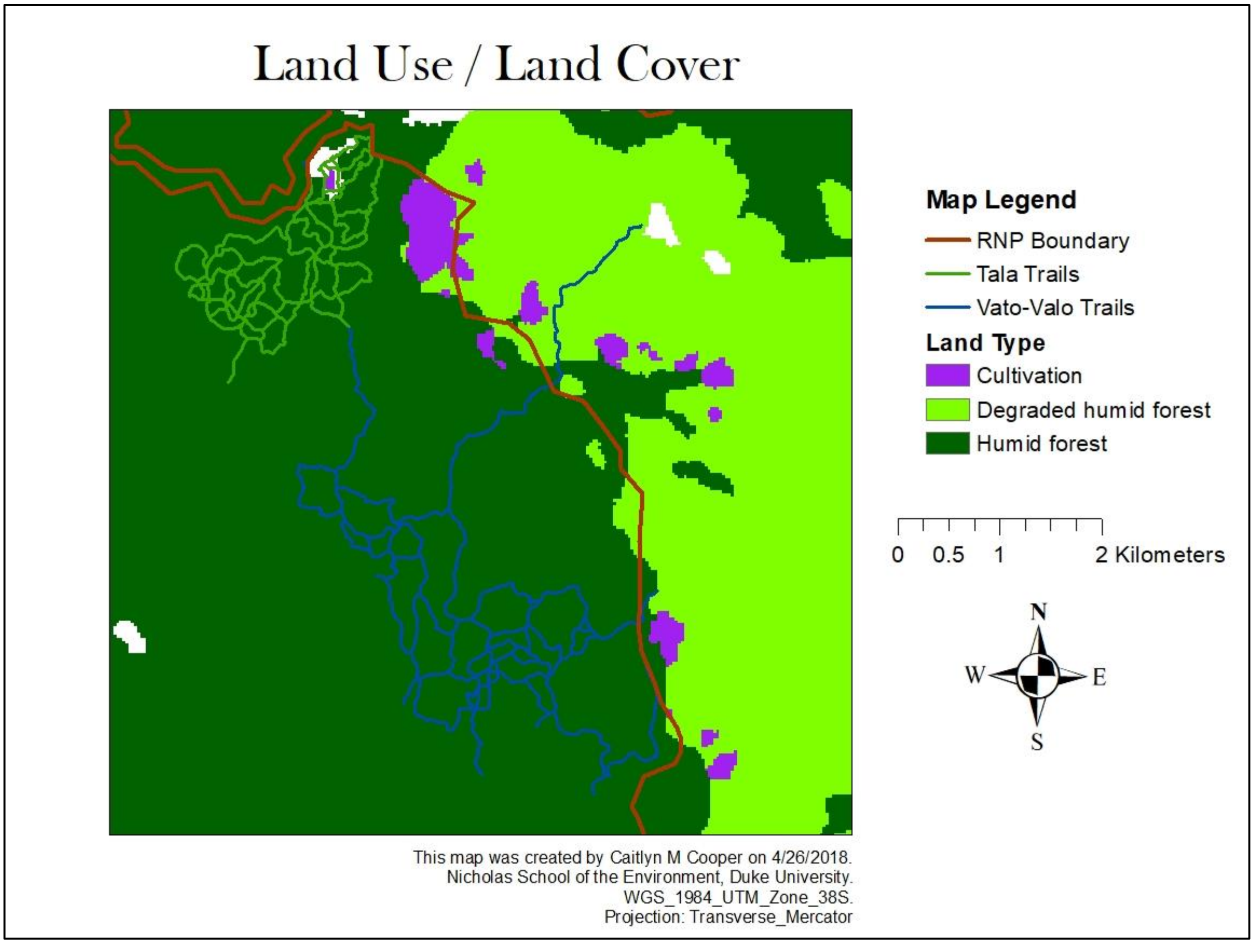

Figure 14: The land cover within the park is mostly humid forest, but some patches of degraded humid forest and cultivation are within the larger humid forest matrix.

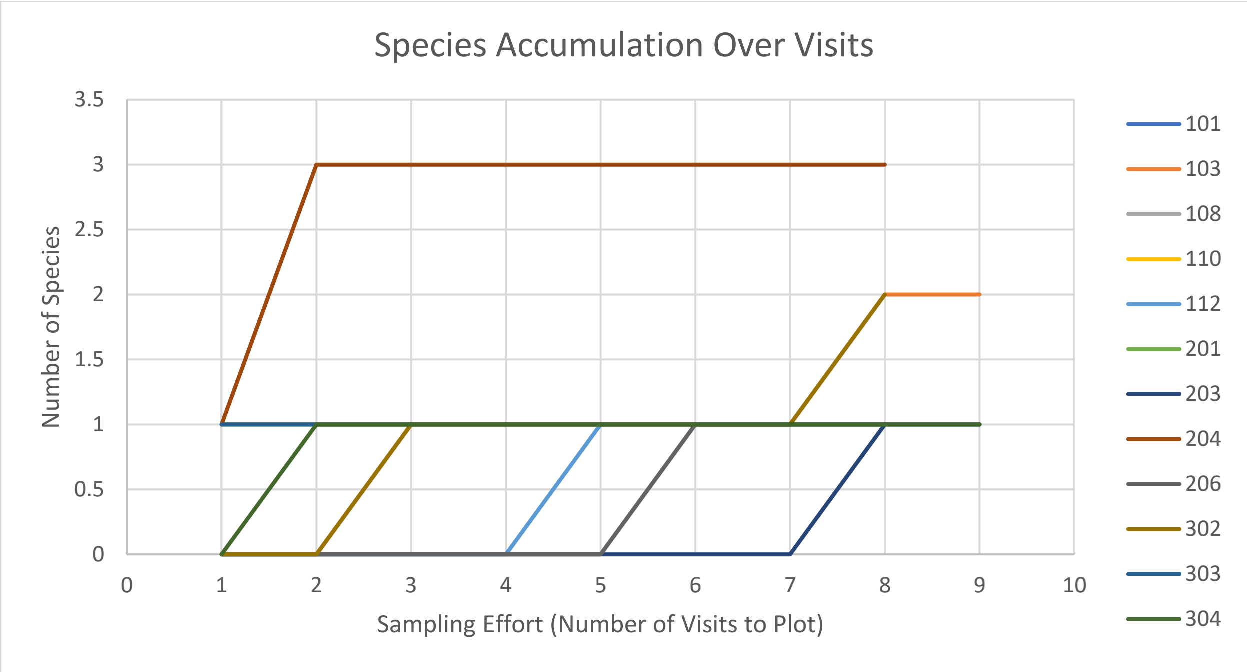

Figure 15: Species accumulation curves of number of new lemur species seen with each new visit to the plot. Plots 101 – 112 are located in Talatakely, Plots 201 – 206 are located in Valohoaka,, and plots 302 – 304 are located in Vatoharanana.

Citations

Atsalis, S., 2000. Spatial distribution and population composition of the brown mouse lemur (Microcebus rufus) in Ranomafana National Park, Madagascar, and its implications for social organization. *American Journal of Primatology*, 51(1), pp.61–78.

Balko, E.A. & Underwood, H.B., 2005. Effects of forest structure and composition on food availability for Varecia variegata at Ranomafana National Park, Madagascar. *American Journal of Primatology*, 66(1), pp.45–70.

Ballhorn, D.J., Rakotoarivelo, F.P. & Kautz, S., 2016. Coevolution of Cyanogenic Bamboos and Bamboo Lemurs on Madagascar. , pp.1–25.

Brooks, T.M., Pimm, S.L. & Oyugi, J.O., 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology*, 13(5), pp.1140–1150. Available at: http://dx.doi.org/10.1046/j.1523-1739.1999.98341.x.

Brown, K.A. & Gurevitch, J., 2004. Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, 101(16), pp.6045–6049. Available at: http://www.pnas.org/content/101/16/6045.full%5Cnpapers3://publication/doi/10.1073/pnas.0401456101.

Bublitz, D.C. et al., 2015. Pathogenic enterobacteria in lemurs associated with anthropogenic disturbance. *American Journal of Primatology*, 77(3), pp.330–337.

Cadle, J.E., 2014. Natural History and Taxanomic Notes on Liopholidophis grandidieri Mocquard, an Upland Rain Forest Snake From Madagascar (Serpentes: Lamprophiidae: Pseudoxyrhophiinae). *Herpetological Conservation and Biology*, 9(2), pp.406–416.

Chen, J., Franklin, J.F. & Spies, T.A., 1992. Vegetation Responses to Edge Environments in

Old-Growth Douglas-Fir Forests. *Ecological Applications*, 2(4), pp.387–396.

Crouse, D. et al., 2015. *Lemur face recognition: Tracking a threatened species and individuals with minimal impact*,

Dudley, N. & Vallauri, D., 2005. Restoration of Deadwood as a Critical Microhabitat in Forest Landscapes. In *Forest Restoration in Landscapes: Beyond Planting Trees*. New York: Springer, pp. 203–207.

Dunham, A.E. et al., 2008. Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur. *Biological Conservation*, 141(1), pp.287–297.

Fish, K.D. et al., 2007. Coprophagy by Wild Ring-Tailed Lemurs (Lemur catta) in Human-Disturbed Locations Adjacent to the Beza Mahafaly Special Reserve , Madagascar. *American Journal of Physical Anthropology*, 69, pp.713–718.

Ganzhorn, J.U., 1995. Low-level forest disturbance effects on primary production , leaf chemistry , and lemur populations. *Ecology*, 76(7), pp.2084–2096.

Gibson, L.A., 2011. The importance of incorporating imperfect detection in biodiversity assessments: a case study of small mammals in an Australian region. *Diversity and Distributions*, 17, pp.613–623.

Glessner, K.D.G. & Britt, A., 2005. Population density and home range size of Indri indri in a protected low altitude rain forest. *International Journal of Primatology*, 26(4), pp.855–872.

Harper, G.J. et al., 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, 34(4), pp.325–333.

Herrera, J.P. et al., 2011. The effects of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. *International Journal of Primatology*, 32(5), pp.1091–1108.

Irwin, M.T., Johnson, S.E. & Wright, P.C., 2005. The state of lemur conservation in southeastern Madagascar : population and habitat assessments for diurnal and cathemeral lemurs using surveys , satellite imagery and GIS. *Oryx*, 39(2), pp.204–218.

Johnson, S.E. & Overdorff, D.J., 1999. Census of Brown Lemurs (Eulemur fulvus sspp .) in Southeastern Madagascar : Methods-Testing and Conservation Implications. *American Journal of Primatology*, 47, pp.51–60.

King, T. et al., 2013. Large-Culmed Bamboos in Madagascar : Distribution and Field Identification of the Primary Food Sources of the Critically Endangered Greater Bamboo Lemur Prolemur simus. *Primate Conservation*, 27, pp.33–53.

Loudon, J.E., Sauther, M.L. & Fish, K.D., 2006. One reserve , three primates : applying a holistic approach to understand the interconnections among ring-tailed lemurs (Lemur catta), Verreaux â€™ s sifaka (Propithecus verreauxi), and humans (Homo sapiens) at Beza Mahafaly Special Reserve , Madagasc. *Ecology and Environmental Anthropology*, 2(2), pp.54–74.

Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27(2), pp.209–220.

Mittermeier, R. a et al., 1992. *Lemurs of Madagascar: An action plan for their conservation 1993-1999*,

Myers, N. et al., 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), pp.853–858. Available at: http://www.ncbi.nlm.nih.gov/pubmed/10706275%5Cnhttp://www.nature.com/doifinder/10.1038/35002501.

Newmark, W.D. et al., 2017. Targeted habitat restoration can reduce extinction rates in fragmented forests. *PNAS*, 114(36), pp.9635–9640.

Overdorff, D.J., 1993. *Similarities, Differences, and Seasonal Patterns in the Diets of Eulemur rubriventer and Eulemur fulvus rufus in the Ranomafana National Park, Madagascar*,

Pfeifer, M. et al., 2015. Deadwood biomass : an underestimated carbon stock in degraded tropical forests ? *Environmental Research Letters*, 10(44019), pp.1–11.

Porter, L.M., 1998. Influences on the distribution of Lepilemur microdon in the Ranomafana National Park, Madagascar. *Folia Primatologica*, 69(3), pp.172–176. Available at: http://dx.doi.org/10.1159/000021580.

Ralison, J.M., Ratsimbazafy, J.H. & Rajaonson, A., 2015. Note sur la présence de Prolemur simus a Ranomafana Est, District de Brickaville. *Lemur News*, pp.6–7.

Rendigs, A. et al., 2003. Relationship between microhabitat structure and distribution of mouse lemurs (Microcebus spp.) in northwestern Madagascar. *International Journal of Primatology*, 24(1), pp.47–64.

Schwitzer, C. et al., 2014. Averting lemur extinctions amid Madagascar's political crisis. *Science*, 343(6173), pp.842–843. Available at: http://www.sciencemag.org/cgi/doi/10.1126/science.1245783.

Tan, C.L., 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (genus Hapalemur) in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 20(4), pp.547–566.

Tecot, S.R., 2008. *Copyright by Stacey Robyn Tecot 2008*.

Watkins, D. SRTM Tile Grabber. Retrieved March 26, 2018, from http://dwtkns.com/srtm/

White, F.J. et al., 1995. Distribution of Ruffed Lemurs (Varecia variegata) in Ranomafana National Park, Madagascar. *Folia Primatol*, 64, pp.124–131.

Worman, C.O.D. & Chapman, C.A., 2006. Densities of two frugivorous primates with respect to forest and fragment tree species composition and fruit availability. *International Journal of Primatology*, 27(1), pp.203–225.

Wright, P., 1995. Demography and life history of free-ranging Propithecus diadema edwardsi in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 16(5), pp.835–854. Available at: http://dx.doi.org/10.1007/BF02735722.

Wright, P.C. et al., 2012. Long-term lemur research at Centre Valbio, Ranomafana National Park, Madagascar. In P. M. Kappeler & D. P. Watts, eds. *Long-Term Field Studies of Primates*. Springer-Verlag Berlin Heidelberg, pp. 67–100. Available at: http://link.springer.com/10.1007/978-3-642-22514-7.