Spring 2014

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Manongarivo Special Reserve, Madagascar**

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7 May 2014
School for International Training
Spring 2014: Madagascar: Biodiversity & Natural Resource Management

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Acknowledgements

The success of this project could not have been realized without the support of several interested parties in Madagascar, to whom thanks are due in advance of this report.

I would first like to extend my thanks to the academic staff of the School for International Training's Biodiversity & Natural Resource Management program in Madagascar for providing a challenging academic and cultural curriculum that served as the springboard for this project: Jim Hansen, Mamy Rajaonah, N'Aina Raevoniaina, Barry Ferguson, Sosony Razafimandimby, and Martine Razafimandimby. Special recognition is due to Barry Ferguson for providing consistent guidance and support as this project topic evolved throughout the semester and for originally suggesting to me the project location.

Thanks are also due to Ms. Leah Glass, Blue Forests Project Coordinator for Blue Ventures Conservation, for serving as the advisor to this project. Without her assistance, all the satellite imagery work associated with this report, including the Google Earth imagery and NDVI values from LandSAT imagery, would not have been possible.

Without the gracious permission of Madagascar National Parks (MNP), I would not have been allowed to enter Manongarivo Special Reserve to conduct this study. In particular I would like to thank Mr. Hamisy Hamidy, *Agent de Réserve* for MNP-Ambanja, and Mr. Lucien, local guide from Analanantsoa, for serving as my guides during my time in the reserve. Their logistical support and knowledge of the local plant communities and species names were invaluable.

I lastly offer my thanks to the locals who live in Beraty and Analanantsoa, near the reserve boundary, for welcoming me into their community and generously providing their knowledge and resources towards my project. The extent of their magnanimity is worthy of higher praise than I can offer here.

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Abstract

This study examines how plant community structure changes across an elevation gradient in Manongarivo Special Reserve, Madagascar. Three vegetation surveys were conducted at each of six different elevations (300m, 500m, 700m, 850m, 1000m, 1150m) on the southern slope of Bekolosy Mountain, near the southwestern border of the reserve. Each of these surveys focused on the diameter, height, and crown position of trees in a $156.25m^2$ plot, as well as the presence or absence of mosses and vines. At each of the six survey elevations, point-quadrat vertical structure data was also collected for the underbrush, up to a maximum height of 2.50m. Average diameter declines noticeably with altitude, from 10.36cm at 300m to 6.66cm at 1150m, with average total height exhibiting a similar but less defined pattern, from 10.74m at 300m to 6.09m at 1150m. Underbrush density increases with altitude, presumably due to an observed decrease in forest canopy closure allowing more sunlight and rainfall to reach the forest floor. Net wooded area also declines with altitude, though population density remains consistent or increases, indicating that smaller trees are more numerous at elevation. Correspondingly, the species diversity of large trees decreases with elevation. Moss coverage also increases as a function of elevation due to an assumed increase in humidity, though vine coverage remains mostly constant. Future research is necessary to measure changes in the abiotic qualities across this gradient, such as changes in average temperature or soil nutrient richness, to identify specific causes for the observed changes in the plant community.

I. Introduction

When used to describe ecosystems, the word "diversity" is quickly connoted with species diversity or the number of species in a given environment, but ecosystems can exhibit equally important levels of diversity with respect to the size, population density, and other functional traits of individuals within the ecosystem (Diaz & Cabido 1997). These traits can often be used as indicators of ecosystem health (Dudley et al., 2006) and of the amount of stress an ecosystem faces (Swenson & Enquist, 2007): underperforming or highly stressed ecosystems are generally comprised of physically smaller individuals at lower population densities than their healthy or less-stressed counterparts (Weiher & Keddy, 1995). Individuals in stressed ecosystems also tend to exhibit less overall diversity or range in their functional traits (Swenson & Enquist, 2007).

Plant community structure, which is here defined as the functional traits of the entire assembly of plants in a given ecosystem, from epiphytes to trees, is highly affected by environmental stress (Benassi et al., 2011). Recent studies have suggested that there are a few key functional traits, including size (Enquist, 2002), leaf area (Wright et al., 2004), and wood density (Swenson & Enquist, 2007), that correlate strongly with the health of the entire plant and can therefore provide proxies through which we can measure ecosystem stress. According to the Weiher & Keddy (1995) hypothesis, plant communities subject to more abiotic stress will be less diverse in size than their less-stressed counterparts, with stressed plant communities presenting as generally smaller. These abiotic stresses can include, but are not limited to, wider temperature ranges or lower minimum temperatures, increased exposure to wind, nutrient-poor soil, and limited rainfall or sunlight (Cierjacks et al., 2008).

Plants growing in mountainous regions, and in particular at high altitude, are subject to many of these stresses (Cierjacks et al., 2008). Their location exposes them to stronger and more frequent winds and to lower yearly temperatures (Gautier & Goodman, 2000). Mountain uplift

events also result in the interiors or summits of mountain ridges being comprised of denser, metamorphic rocks, creating a rockier and less nutrient-rich soil than areas downslope that benefit from more fertile soil and nutrient runoff from upslope (Swenson & Enquist, 2007).

Several studies have indeed found that plants at higher elevations exhibit characteristics consistent with the Weiher & Keddy hypothesis. Wood density, or the ratio of dry mass to living green tissue in a tree trunk, is higher and more diverse in tropical lowland rainforests than in highland rainforests (Swenson & Enquist, 2007). Vertical growth rates of trees decline with altitude, in part due to the stresses associated with altitude and in part due to a decrease in light competition associated with a decrease in canopy cover (Coomes & Allen, 2007). Tree saplings also have a lower establishment rate at altitude, where they are unable to compete with larger trees for enough nutrients from the already nutrient-poor soil (Cierjacks et al., 2008). Interestingly, despite the decline in functional traits of trees at altitude, moss biomass increases with altitude, presumably due to higher humidity at those elevations (Benassi et al., 2011).

Many of Madagascar's rainforest ecosystems, such as those found in Ranomafana National Park near Fianarantsoa or in Kianjavato Classified Reserve in the east, are spread across a wide elevation range and are therefore an ideal environment for studying how the functional traits of plant communities change across elevations. As a result of their location in the tropics and of being isolated from other land masses for over 88 million years, many of these forests also exhibit a high level of both national and local endemism (Gautier & Goodman, 2003)**.** An understanding of whether or not these ecosystems follow the Weiher & Keddy (1995) hypothesis would both bolster the current data set on plant change across altitude and provide insight into whether or not endemic or partially endemic forests compensate for altitude in the same fashion as more widely distributed species.

Manongarivo Special Reserve, a 32,000 hectare protected area established in 1956

approximately 40km south of Ambanja,

Madagascar (Fig. 1), contains a not-often

studied rainforest ecosystem well-suited to

an elevation range study (Gautier &

Goodman, 2002). Situated in a hot and

humid tropical climate, with an average of

2000mm of rainfall per year and an average

yearly temperature of 26°C (Hufty 1.2), the

reserve itself is comprised almost

Fig. 1: Google Maps image indicating the location ("A") of Manongarivo Special Reserve, Madagascar.

exclusively of tropical rainforest (Gautier & Goodman, 2000). "Manongarivo" translates from

Malagasy as "thousand summits" (Hufty 1.2), and the reserve appropriately has a high elevation

gradient, starting at approximately 50m above sea level and culminating at the peak Ansatrotro at

1876m (Hufty 1.3). Moreover, this entire elevation range is spread across a small latitudinal area,

ensuring that high-altitude plants are both accessible and fully exposed to stresses like wind and

erosion (Gautier & Goodman, 2002). Some 28% of the reserve is lowland forest (<800m),

another 60% mid-altitude (800-1600m), and 11% highland forest (>1600m) (Hufty 1.3).

Manongarivo's rainforest also has few outside impacts that could affect how the plant

community changes across elevation. A low level of human use, particularly at high elevations,

ensures that any observed changes in plant community structure are the result of environmental

influences and not human impact (Hufty 4.1). Deforestation in Manongarivo has been restricted

to low elevations, with slash-and-burn agriculture beginning at the lowest elevations, moving

slightly upslope, and then retreating back downslope again as the downslope soil rejuvenates

(Hufty 4.1). The primary economic activity of locals living in adjacent villages is rice farming,

followed by the production of other agricultural products including vanilla and cacao. All of these activities require fertile soil and are therefore restricted to low elevation (Ranaivonasy & Rakotoarisoa, 1999). With respect to tourism, less than ten visitors enter the reserve each year, making the tourist or visitor impact on the forest negligible ("Plan de Sauvegarde Sociale"). A high level of species diversity in the park – a total of over 200 plant species – further ensures that any observed changes in the plant community over an elevation range are truly the result of a change in community functional traits and not of a change in a small subset of species ("Reserve Special Manongarivo").

Given the natural advantages of Manongarivo Special Reserve towards understanding how functional traits of plant communities change across elevation, the objective of this study is to determine whether Manongarivo's rainforest follows the Weiher & Keddy hypothesis with respect to an elevation gradient and to quantify the change in forest functional traits across said gradient. A secondary objective is to determine whether plants growing on steeper slopes, a presumably more stressful environment, follow the Weiher & Keddy hypothesis with respect to plant communities growing on flat surfaces at equal elevations. To ensure a complete sample of the plant community, trees, underbrush, and epiphytes are all considered as part of this study. In keeping with an ethic of forest conservation, the functional traits of interest in this study are solely those that can be measured without cutting or otherwise damaging any trees and include but are not limited to canopy closure, tree diameters, and tree heights. All research was conducted during three weeks in April 2014.

II. Methods

    2.1 Study Site

    The southwestern edge of the park was chosen as the study site due to both its isolation and to the presence of taller mountain peaks while still remaining proximate to available food and supplies in the nearby villages of Beraty and Analanantsoa. This edge of the park includes a "*zone tampon*," in which it is permitted for locals to cultivate agricultural products and collect resources without clearing or burning away forest ("Plan de Sauvegarde Sociale"). A small fraction of this low-altitude forest on the southwestern boundary of the park is second-growth forest due to historical deforestation by local villagers. Adjacent to this zone is the "*noyau dur*" in which agriculture, lumber production, and other human industries are strictly prohibited, leaving a largely undisturbed forest landscape ("Plan de Sauvegarde Sociale").

    Bekolosy Mountain, where this study was conducted, is situated in the *noyau dur* at the northeastern boundary of the *zone tampon*, so that the mountain is generally accessible yet remains free of any human pressures since at least the establishment of the park (Fig. 2). Bekolosy, in conjunction with Andaimpotsy Mountain, comprises one of the two major mountain ridges in the park, the other being Ansatrotro (Hufty 1.2). The upper slopes of the mountain have been historically undisturbed since well before the park's establishment due to the

Fig. 2: The location of Bekolosy Mountain, signified by a yellow dot, within Manongarivo Special Reserve.

availability of resources on lower slopes and the difficulties associated with climbing and descending the mountain with resources and equipment. The mountain itself stands approximately 1300m tall, with a base at approximately 400m and a gentle slope extending

further towards the Manongarivo River. Bekolosy is crested by a river of the same name, which begins near the mountain's summit, falls down the mountain's western slope, and is ultimately a tributary to the Manongarivo River.

Work was carried out at six different elevations along the south and southwestern slopes of Bekolosy. Because the upper slopes of Bekolosy are primary, original-growth forest, the study sites at all elevations were chosen so that all work was carried out in primary forest. The lowest elevation studied, 300m above sea level, was on an adjacent plain approximately 1km from the mountain proper, and the highest elevation, 1150m above sea level, represents the highest feasible and reasonably accessible study site yet remained some 150 vertical meters shy of the mountain's true summit. The four intermediate elevations – 500m, 700m, 850m, and 1000m above sea level – occur on the mountain face itself.

2.2 Vegetation Survey Plots

At each of the six study elevations, vegetation samples were carried out in three 12.5 x 12.5m plots. Plots were delineated using rope and tape measures. GPS coordinates were taken for each plot, including an altitude measurement. If the GPS altitude reading for a plot was inconsistent, multiple readings were taken over the course of two to three hours and the readings were averaged to determine the elevation. All plots were placed within ±20m of the target study elevation: for example, all plots defined as "500m" fall within 480-520m. When the topography at a given elevation allowed for it, attempts were made to place the three plots on slopes of different grade, so that at least one plot is located on a generally flat area and another on a steeper face. Attempts were also made to place the plots on both east- and west-facing slopes.

Notable physical attributes of each plot, including runoff stream trails or large rocks, were recorded, as well as any evidence of recent human disturbance or animal use. The slope of each plot was qualitatively defined as either "steep" or "flat or slightly graded," and for the steep

plots, the cardinal direction towards which the slope was oriented was recorded. Canopy closure, defined by Newton (2007), was estimated by visual inspection at each of the four corners of the plot and then averaged. The three canopy closure values from the plots at each elevation were subsequently averaged to obtain one canopy closure value per elevation. LandSAT images from each of the eighteen plot locations were used to calculate local Normalized Difference Vegetation Index (NDVI) values to assess chlorophyll content and light reflection.

In each 12.5m x 12.5m plot, all trees with a diameter at breast height (DBH) greater than or equal to 5.0cm were sampled, where breast height is defined by Newton (2007) as 130cm above the ground. Vernacular species names of each tree were provided by a local Sakalava guide, Lucien, from the village of Analanantsoa. Circumferences at breast height were measured with a tape measure, and height of first branch and total height were measured with a tape measure or, when necessary, estimated using a clinometer. Following the practices of Newton (2007), the crown position of each tree was defined as either "dominant," "codominant," "intermediate," or "suppressed," based on visual inspection. Any remarkable physical characteristics of observed trees, including any non-vertical growth patterns, were also recorded.

Within each 12.5m x 12.5m, plot, a 5m x 5m subplot was constructed in which all trees with a diameter at breast height less than 5.0cm were sampled (Fig. 3). The same measurements were taken for these trees as for the trees described in the preceding paragraph.

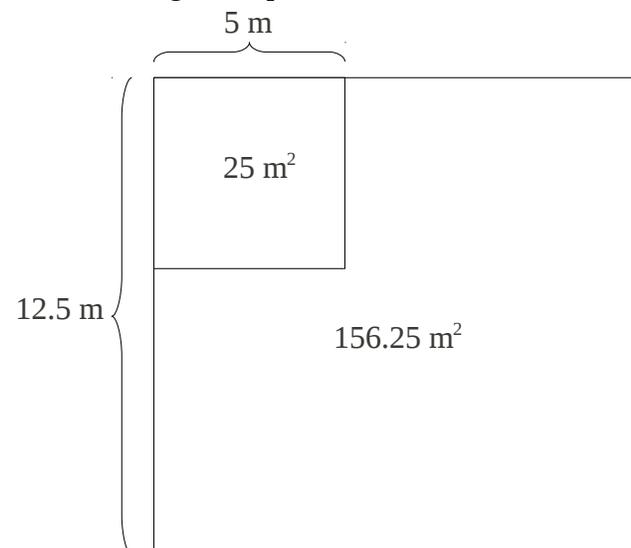For all trees measured within a plot, circumferences were converted to diameters

Fig. 3: A schematic representation of the layout of a single plot. The 5x5m subplot is contained within the larger 12.5x12.5m plot.

at breast height. The net wooded area, defined as the sum of the areas of all the tree trunks on a plot (Fig. 4), was calculated independently for the 12.5m x 12.5m plots of trees with DBH ≥ 5.0cm and for the 5x5m subplots of trees with DBH < 5.0cm. Population density of trees within a plot was similarly calculated separately for the two tree sizes and then added together to find a population density value for all trees. Relative abundance of species was calculated from a list of all the trees in all three plots at each elevation, including subplots. Vernacular names of species were converted to scientific names when possible using Rakotoarisetra (2001), Stiefel (2001), and Petitjean (1992).
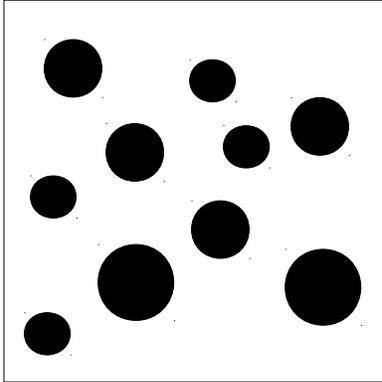

Fig. 4: Schematic indicating the calculation of net wooded area, defined as the area of all the tree trunks (black) within the area of a single plot (white).

2.3 Spatial Distribution of Large Trees

At the 300m, 700m, 850m, and 1150m study sites, a point-centered-quarter analysis, described by Gautier et al. (1994), was performed on the ten largest observable trees with a diameter at breast height greater than or equal to 30.0cm. Center trees were identified by visual inspection while walking through the study area. The distance between the center tree and the closest adjacent tree in each of the four quadrants delineated by the four cardinal directions, as well as the distance between the center tree and the next closest tree with a diameter at breast height greater than or equal to 21.0cm, was measured (Fig. 5). For the center
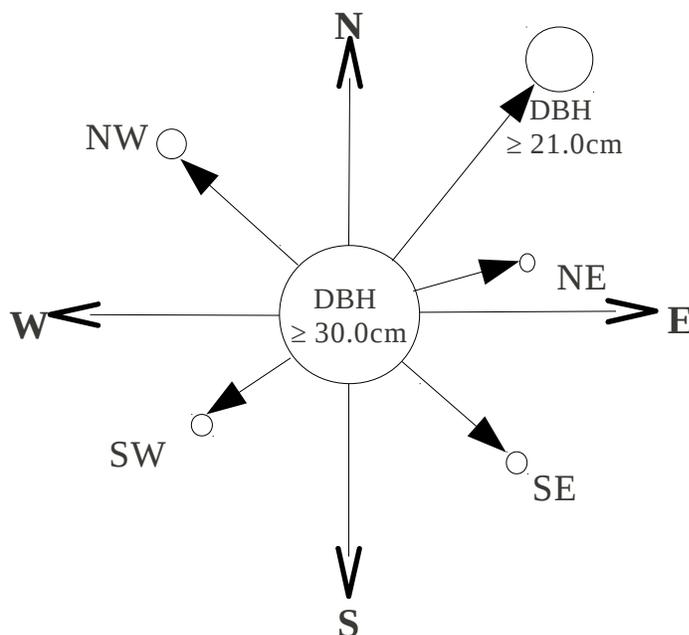
Fig. 5: Schematic indicating how the point-centered quarter (PCQ) analyses were conducted.

tree and each of these five neighbors, the same measurements were taken as for the trees in the vegetation survey plots: vernacular species name, circumference, height of first branch, total height, crown position, and remarkable physical features.

To ensure an appropriate breadth of data, none of the six trees that were sampled in one single point-centered quarter analysis were part of a subsequent point-centered analysis. In this way no tree is represented twice in the data set.

2.4 Underbrush Vertical Structure

At all six study elevations, underbrush vertical structure was studied using the point-quadrat method also described by Gautier et al. (1994). Every 1m along a 50m transect, a post of height 2.5m was erected vertically. Every height above the forest floor at which any vegetation touched the post was recorded, up to a maximum height of 2.5m. No vertical structure measurements were taken for plants or trees taller than 2.5m. Transects were kept as straight as possible and as constant elevation as possible given the surrounding topography, and feasible transect sites were chosen from visual inspection of the study area.

2.5 Epiphyte Presence Study

To assess the epiphyte community change across elevations, a running tally of trees covered with moss or encircled by vines was kept of every tree sampled at each elevation. To qualify as "moss-covered" at least 30% of a tree trunk at breast height needed to be covered by moss, a determination made qualitatively. "Vine-covered" trees were those that were encircled at least two times by one or more vines, regardless of vine species or size. This tally was kept of all trees sampled, whether they were sampled in a vegetation survey plot or as part of a point-centered quarter analysis. Trees that were part of both a vegetation survey and a PCQ analysis were not double-counted.

III. Results

3.1 Vegetation Survey Plots

Due to the difficulties associated with climbing the mountain, all vegetation survey plots were placed along a single north-south ridge rising from the southern side of the mountain towards the summit (Fig. 6). With the exceptions of the 500m and 850m elevations, where no flat or slightly graded areas could be found within the elevation range, plots at each elevation were divided between one or two "flat" and one or two "steep." Table 1 presents a brief list of the plots, their elevations, and their topographical classification.

Fig. 6: Google Earth image indicating the location of vegetation survey plots at 500m elevation and above. 300m plots are too distant to appear at this scale.

The average diameter of all trees decreased consistently with altitude, from 10.36cm to 6.66cm (Fig. 7). When trees with a DBH $\geq$ 5.0cm are considered separately from trees with a DBH < 5.0cm, the decrease in overall average diameter is seen to be due primarily to a significant decrease in

Study Elevation (m)	Plot	Elevation (m)	Topography
300	1	289	flat
	2	305	flat
	3	297	steep
500	4	520	steep
	5	507	steep
	6	509	steep
700	7	692	steep
	8	710	flat
	9	693	flat
850	10	866	steep
	11	838	steep
	12	844	steep
1000	13	1014	flat
	14	1010	steep
	15	1008	flat
1150	16	1145	flat
	17	1146	steep
	18	1150	flat

Table 1: List of plots and their topographical classifications.

the average diameter of DBH $\geq$ 5.0cm trees (Fig. 7). The average diameter of trees with a DBH <

5.0cm decreases slightly from 3.70cm at 300m before rising again to 2.90cm at 1150m. Overall diversity of diameters also decreases noticeably with altitude, with the first and third quartile averages, particularly of trees with a DBH > 5.0cm, shifting noticeably closer to the
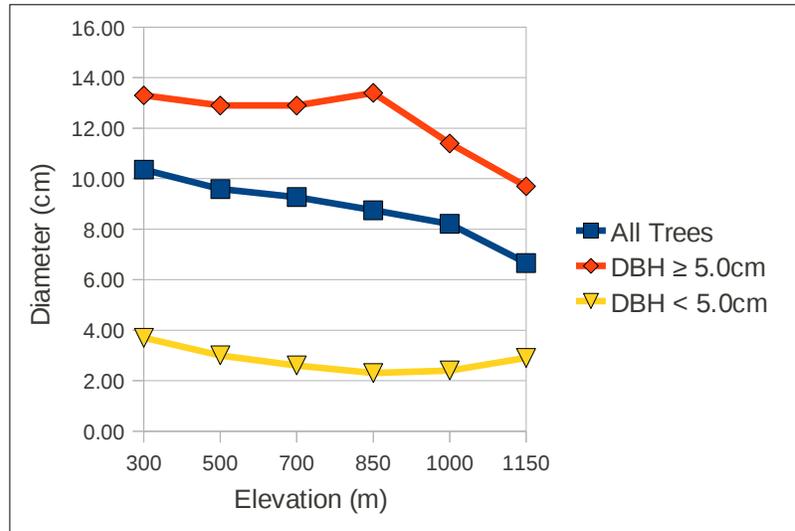

Fig. 7: Average diameter of all trees across elevations, presented both as an overall average and as components based on DBH.

overall average (Fig. 8). Maximum observed diameter exhibits a similar decrease with altitude (Fig. 8), with the largest observed tree occurring at 500m (DBH = 58.6cm).
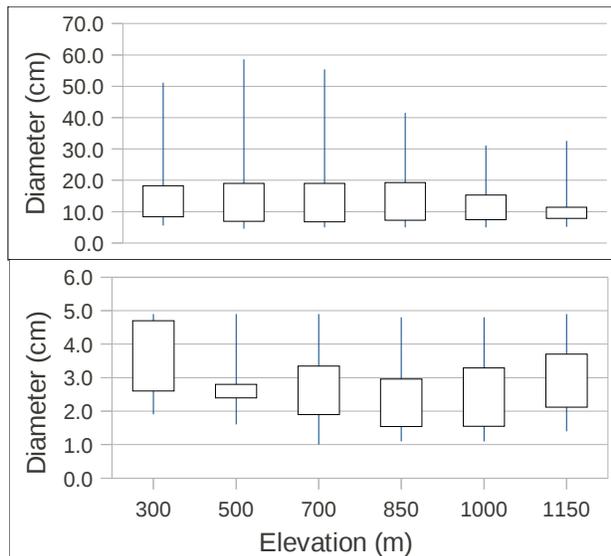

Fig. 8: Box and whisker plots indicating the change in first and third quartile averages of diameter at breast height across elevation. Boxes extend from first to third quartile average; lines extend to maximum and minimum values. Top, all trees with DBH ≥ 5.0cm; bottom, all trees DBH < 5.0cm.
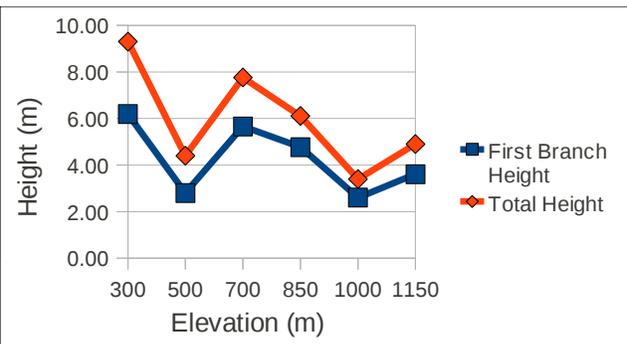
Fig. 9: Average height of first branch and average total height of all trees.

Height of first branch and total height did not exhibit any readily definable trend with altitude. Both values decrease significantly from 300m to 500m before rising again to 700m, after which they decline steadily before rising briefly at the summit (Fig. 9). However, trees observed at 1150m are appreciably shorter and have lower first branches than trees observed at 300m. Height of first branch closely follows

Fig. 10: Box and whisker plots indicating the change in first and third quartile averages of height of first branch (black boxes) and total height (white boxes) across elevation. Boxes extend from first to third quartile average; lines extend to maximum and minimum values. Top, all trees with DBH ≥ 5.0cm; bottom, all trees DBH < 5.0cm.
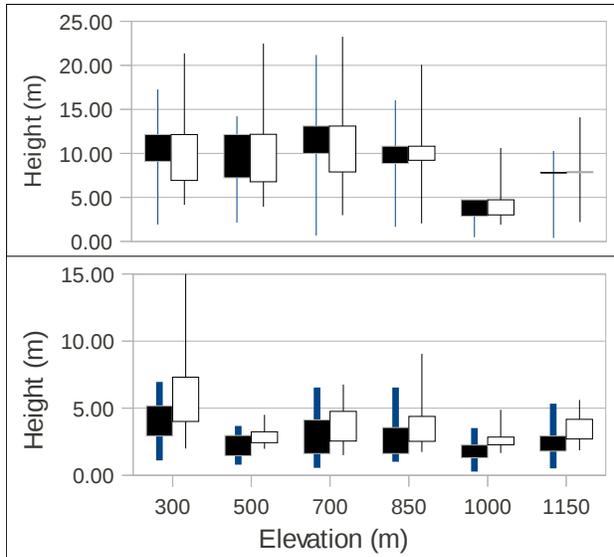
total height, such that the vertical distance between the first branch and the crown of a tree does not change appreciably with altitude. As observed with tree diameters, overall height diversity decreases with altitude, with first and third quartile averages approaching the overall average (Fig. 10). Maximum observed height generally decreases with altitude; the tallest observed tree occurs at 700m (branch = 15.44m, height = 23.25m). Interestingly, the tallest tree did not also have the greatest height of first branch: the greatest height of first branch was instead observed at 300m (branch = 17.27m, height = 19.95m).

Concordant with the observed decrease in tree diameters and weak decrease in tree heights, canopy closure declines steadily with altitude (Fig. 11), from 87.5% at 300m to 36.7% at 1150m. Despite the decrease in canopy coverage, NDVI values exhibit no similar trend, with the NDVI value at 300m roughly equal to the NDVI value at 1150m (0.408 vs 0.392, respectively) (Fig. 12), suggesting that at high elevations plants that do not rise to the stature of the tree canopy are compensating for the light absorption provided by trees at lower elevations. Net wooded area increased slightly to

Fig. 11: Canopy closure across elevation.

Fig. 12: NDVI index across elevation.

850m before declining significantly to 1150m (2.13m^2 at 300m vs. 1.23m^2 at 1150m) (Fig. 13).

The slope of a plot had a small but noticeable effect on the tree size within a plot. At the four elevations at which both flat/graded and steep plots were established,

Fig. 13: Net wooded area across elevation.

the average diameter and average total height of all trees is smaller on the steeper plots (Fig. 14).

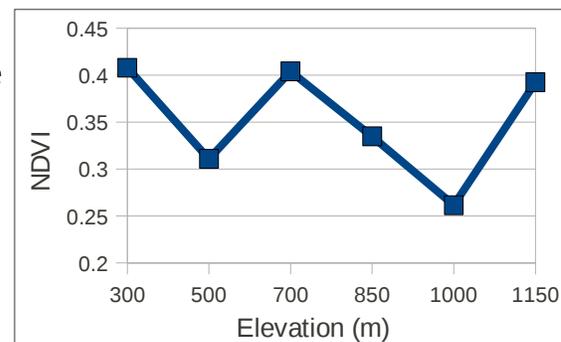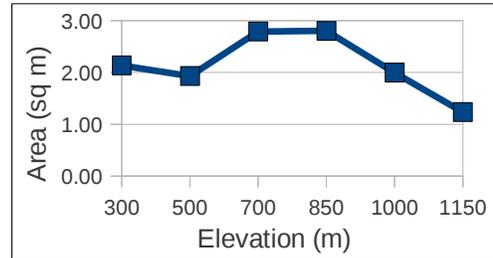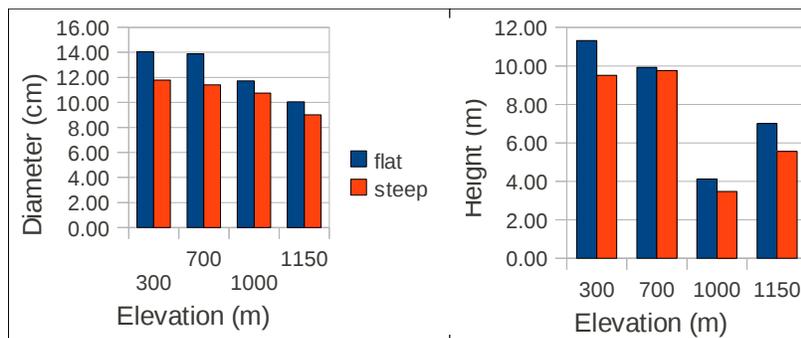**Fig. 14:** Comparison of tree functional characteristics based on slope of plot. Left, DBH; right, total height. Flat plots in blue, steep plots in red.

Trees on steeper slopes exhibit diameters and heights roughly 80-90% of those on flat slopes. East-facing plots were not significantly different from west-facing plots.

No significant trends were observed regarding the crown positions of trees. Elevation had no effect on the proportion of trees reaching a certain crown position. Average diameter, height of first branch, and total height of trees at each crown position declined with altitude following the same pattern described earlier for all trees sampled in this study, though a majority of the decline was found in dominant trees. Similarly, no consistent trend was observed with respect to population density, but the population density at 1150m was noticeably higher than at 300m (0.40 vs. 0.29 trees/m^2, respectively).

Number of species observed in plots at each elevation exhibited no significant change (Table 2), though the relative abundance of several more common species changed significantly as a function of elevation. In particular, *Erythroxylum sphaeranthum* (vernacular = "*Malaimsisiky*"), which accounted for one-fifth of the trees at 300m, is completely absent at the summit. "*Anivon*," *Alberta sambiranensis* (vernacular = "*Honkoala*"), and "*Kitrotrotrotroko*," all

of which are
absent at low
elevations,
account for a
noticeable
portion of the

Species Name	300	500	700	850	1000	1150
"Anivon" (f. PALMIERS)	0.00%	0.00%	0.00%	0.00%	3.02%	4.91%
Garcinia pauciflora	2.52%	1.56%	2.38%	4.93%	4.74%	5.36%
Alberta sambiranensis	0.00%	0.00%	0.00%	0.00%	3.88%	4.91%
"*Kitrotrotrotroko*" (unknown)	0.00%	0.00%	0.00%	0.00%	0.86%	2.68%
Erythroxylum sphaeranthum	20.75%	0.00%	2.86%	1.90%	0.00%	0.00%
"Trotroko" (unknown)	4.40%	0.00%	0.48%	1.41%	0.43%	0.00%
"Tsongavatrondra" (unknown)	0.00%	20.31%	4.29%	7.75%	0.00%	0.00%
Total # of Species Observed	64	61	72	66	69	67

Table 2: Relative abundance of some of the more common species observed during the vegetation surveys. Total number of species observed at each elevation appears on the bottom. Quotation marks introduce species vernacular names if no scientific name was available.

trees at higher elevations. *"Tsongavatrondra"* is absent from both low-altitude and high-altitude plots but account for a significant portion of trees observed at mid-elevations. Several other common species, including *Garcinia pauciflora* (vernacular = *"Hazininy"*) and several trees of the genus *Homalium*, persist at all elevations.

3.2 PCQ Analysis

The average diameters, heights of first branch, and total heights of the four trees most closely associated with the central large trees in the PCQ analysis follow the same general trends as those in the vegetation surveys, and so will not be discussed at length here beyond restating the general decrease in those values. The average distance between large trees and their nearest neighbors exhibited a
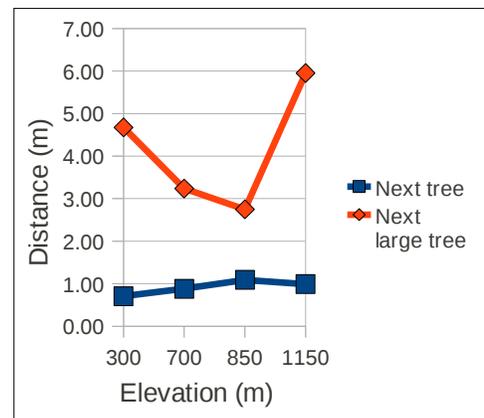
Fig. 15: Average distance between PCQ center tree and the nearest neighbors (blue line) and the next largest tree (red line) as a function of elevation.

negligible increase with altitude, from 0.71m at 300m to 1.00m at 1150m, while the distance between large trees and the next large tree followed no definable pattern, decreasing from 300m (4.68m) to 850m (2.75m) before increasing to 1150m (7.96m) (Fig. 15).

The number of species represented in the set of ten central trees decreases noticeably with elevation. At 300m, ten separate species were the subject of a PCQ analysis; at 1150m, only four species were central trees (Table 3). Three of the four central species in the 1150m PCQ analysis

Fig. 16 (above): Vertical structure diagrams at each of the six study elevations.
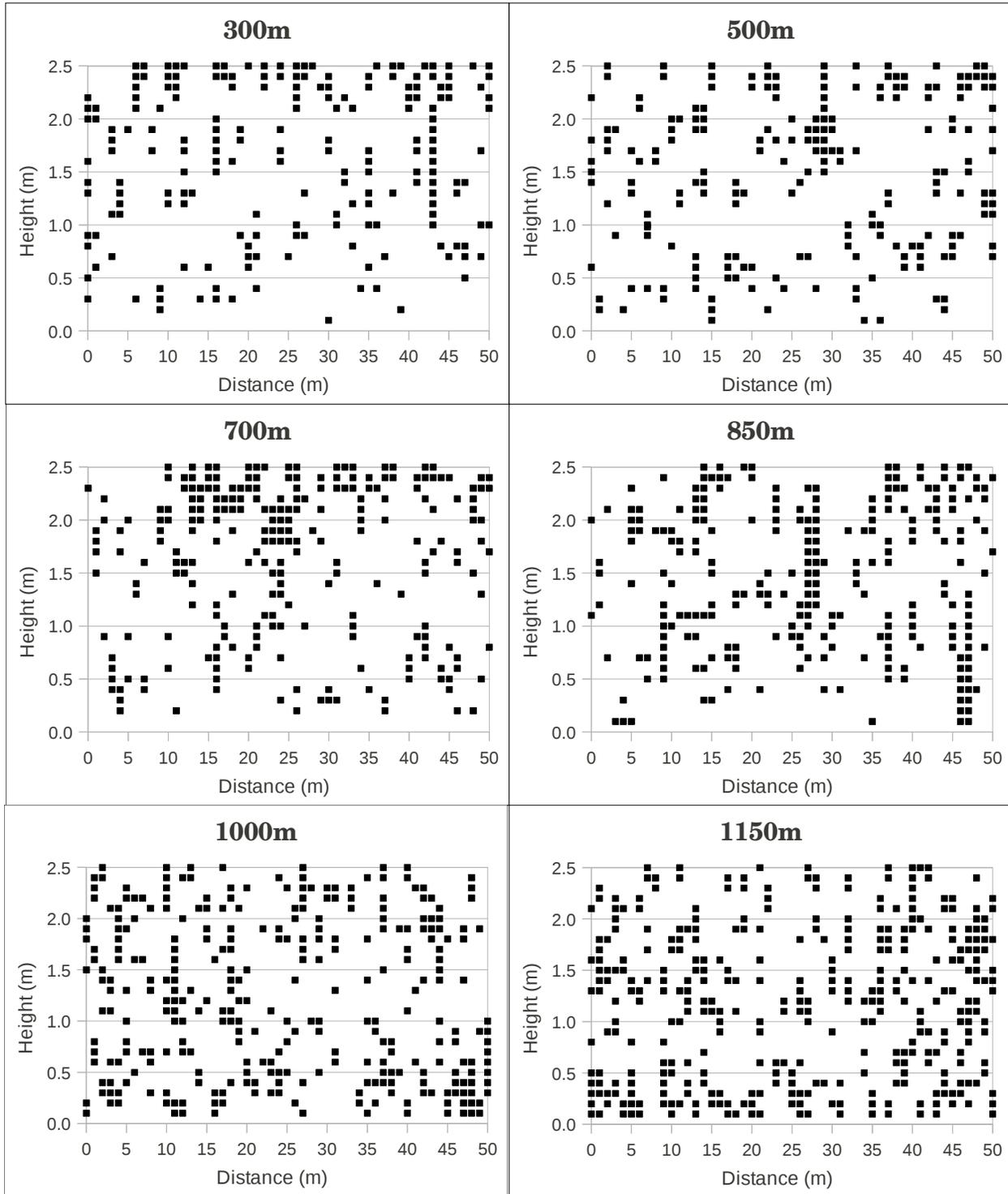
Elevation (m)	# of Points	Prop ≤ 1.5	Prop > 1.5
300	190	0.57	0.43
500	201	0.49	0.51
700	238	0.38	0.62
850	248	0.52	0.48
1000	296	0.60	0.40
1150	339	0.65	0.35

Table 4 (left): Tabulated data, including proportions of underbrush falling within certain classes, for the vertical structure diagrams above.

were also central species at low elevations.

3.3 Underbrush Vertical Structure

The density of the forest underbrush and understory, measured up to a maximum height of 2.5m, increased steadily with elevation. This is evident not only in a qualitative assessment of

Elevation (m)			
300	**700**	**850**	**1150**
C. parviflorum	*C. parviflorum*	*C. parviflorum*	*C. parviflorum*
Haramy	Haramy	Haramy	Haramy
M. boivinii	*M. boivinii*	*M. boivinii*	*M. boivinii*
B. merana	*B. merana*	Lalona	Lalona
Rara	Rara	*T. perrieri*	
E. sphaeranthum	Taovony		
Mandronahefaka	Adabo		
Terminalia sp.	*A. fallax*		
Vampiro			
Voara			

Table 3: List of tree species that were large, central trees in the PCQ analyses, by elevation. Species not italicized indicate vernacular names.

vertical structure transect diagrams (Fig. 16) but also from the increasing number of independent points on the vertical structure diagrams as elevation increases (Table 4). At lower elevations, underbrush density is concentrated between 1.5-2.5m and is primarily due to the crowns of shorter trees and saplings. Above 850m, underbrush between 0 and 1.5m tall becomes more common, to the point where the proportion of low-level underbrush exceeds the proportion of high-level underbrush (0.65 vs. 0.35, respectively) (Table 4).

3.4 Epiphyte Study

The overall presence of epiphytes generally increased with altitude, from 5.48% of trees covered at 300m to 30.60% at 1150m (Fig. 17). Epiphyte composition shifted from a vine-favored environment at lower elevations to a moss-favored environment at high elevations, with the percentage of moss coverage exceeding the percentage of vine coverage starting at 1000m (18.03 vs. 4.10%).

Although species inventories were not taken, the vine community exhibited a qualitatively observable species shift at approximately 900m elevation. Below 900m, the vine species *ravintampiny* is abundant and the species *valatrahako*

Fig. 17: Epiphyte coverage as a function of elevation.

is absent. Between 900m and 1000m the two species coexist, and above 1000m the vine community is dominated by *valatrahako* and devoid of any *ravintampiny*.

IV. Discussion

The observed overall average decline in tree diameter as a function of elevation fits the trends described by Swenson & Enquist (2007) insofar as a key functional value trait of a high-altitude tropical forest is lower than that of a low-altitude tropical forest. Although height of first branch and total height exhibited a less consistent decline, the slight overall decrease similarly supports the Swenson & Enquist (2007) trend. If we attribute the unexpectedly low heights measured at 500m elevation to the extremely steep slope of those plots, recognizing that steeper plots were found to have measurably shorter and narrower trees and clinometer-based height measurements in steep areas are subject to greater error due to the difference in height between the observer and the tree, the decline in overall height becomes more consistent with elevation. Higher-altitude trees in Manongarivo Special Reserve thus exhibit smaller size metrics than low-altitude counterparts, a finding corroborated by a similar study by Raharimalala (1991) performed across a narrower elevation range also on the Bekolosy mountain chain.

The decline in these functional trait values also supports the Weiher & Keddy (1995) hypothesis, as the overall diversity in diameter, height of first branch, and total height declines with elevation to the point where the first and third quartile average diameters are not far from the overall average diameter. Less diverse values for diameter and height, coupled with the overall declines in those values, suggest that the rainforest on Bekolosy's southern slope is, as expected, exposed to the stresses associated with elevation: wind, wider temperature range, increased erosion, less nutrient-rich runoff, and rocky or nutrient-poor soil. Qualitative observations of the soil at the high-elevation study sites indeed indicate that the high-elevation soil is rockier and presumably less fertile than low-elevation soil. Wind also plays a qualitatively observable role, as a greater proportion of trees at high elevation were growing at a significantly tilted angle to the ground, which I infer to be the result of wind tilting or overturning the tree.

Consistently lower diameter and height measurements for trees on steeper slopes further supports the Weiher & Keddy (1995) hypothesis, with the assumption that steeper slopes provide a more stressful environment due to higher erosion pressure and greater difficulty in establishing a root system. The lack of any distinguishing difference between east- and west-facing slopes is not unsurprising, given that they receive approximately equal amounts of sunlight at an approximately equal incident angle. A future study examining the plant community on a north-facing slope would be valuable to determine if a north-facing slope presents with slightly larger functional value traits than a south-facing slope due to a higher incident angle of sunlight.

Average and maximum diameter values at 300m (13.3cm and 51.6cm, respectively) are comparable to values measured by D'Amico & Gautier (2000) at 220m elevation in a lowland plateau forest southwest of Bekolosy. However, average total height at 300m (10.76m) is distinctly below the 15-20m measured by D'Amico & Gautier (2000) despite being at a comparable elevation. While a portion of this decline could be attributed to the different topographical positions of the plots on a plateau versus adjacent to a mountainside, this might also suggest that the 300m plots in this study have been disturbed in the more distant past, to the extent that the forest is still in the process of regenerating even though no disturbance was visually observed. If this is true, a satellite-based analysis of historical human use patterns, like the one performed by Hufty 4.1, would allow us to both determine if the 300m plots in this study have indeed been historically disturbed and to find a less disturbed location for a 300m plot to ensure all plots are placed on primary forest.

Declining canopy closure with elevation matches the trend described by Coomes & Allen (2007). The lower canopy closure at high elevations may also contribute to lower size metrics; Coomes & Allen (2007) note that with a less dense canopy, trees face less competition for light and therefore have less pressure to grow larger to outcompete their neighbors. Future analyses of

tree growth rates at high versus low elevations on Bekolosy are necessary to support or refute this hypothesis, with the expectation that high-altitude growth rate would decline if there was less competition between trees.

Although canopy closure decreased consistently with elevation, the NDVI values exhibited no similar trend, indicating that at all elevations there is roughly equal photosynthetic activity or chlorophyll content. This consistency can be attributed largely to the increasing underbrush density with elevation, evident in the vertical structure diagrams. With lower canopy closure, more sunlight and rainfall can penetrate to the forest floor, facilitating the growth of the herbaceous understory. The understory, in turn, compensates for the photosynthetic activity being lost from the shrinking canopy cover. No climate data was taken during this study, but higher elevations are often more humid, and the increased humidity may also facilitate understory growth at these elevations.

The lack of any significant shift in photosynthetic activity, as measured by the NDVI, could also be the result of not surveying plants at a high enough altitude to truly be including the highland ecosystem. In a study on Ansatrotro peak, Messmer et al. (2002) found that no definable ecosystem shift occurred until 1600m elevation, where dense rainforest slowly began to be replaced by a more savannah-like plant community. It is possible that the present study does not attain a high enough elevation to observe any significant ecosystem shift and therefore any significant shift in whole-ecosystem characteristics like NDVI. However, by staying within the same ecosystem, evident by the consistent number of overall species observed and the general persistence of most of those species across all elevations, this study operated within a single plant community and therefore observed a true change in key functional traits with elevation and not a change in traits associated with a major species or ecosystem shift.

The NDVI values measured in this study are themselves subject to some doubt due to

topography shadow on the LandSAT images from which they were calculated. Because this study was conducted on a relatively steep southern-facing mountain slope, small valleys or downslope mountain regions were shaded from the sun by the upslope portion of the mountain, which in turn may have depressed the NDVI values at lower elevations. Measuring NDVI indexes from equivalent elevations on a slope more exposed to sunlight would indicate whether the values from the southern slope of Bekolosy are depressed, in which case NDVI might actually decrease with elevation, or if the relatively constant NDVI is in fact a consistent trend across all slopes of the mountain.

The slight decrease in net wooded area, coupled with the insignificant change or possible mild increase in population density, suggests that the number of smaller trees increases with altitude. If the number of trees in a defined area is increasing, but the area covered by those trees is decreasing – a fact corroborated by the decreasing overall average diameter – we can assume that trees present in higher-elevation plots are generally smaller and more numerous. Although this pattern matches that described by Cierjacks et al. (2008) for a South American palm, and smaller trees at high altitude are also expected given the stresses of elevation, increased density is less expected if we assume that higher-altitude soil is rockier and more nutrient-poor. It is possible that many of these smaller trees are currently being crowded out by other neighboring trees, which would corroborate the low sapling establishment rate at altitude observed by Cierjacks et al. (2008), but longer-term study of tree survival rates in these plots would be necessary to confirm this hypothesis.

The increasing net wooded area also contradicts results obtained by Messmer et al. (2002) in a series of plant plots on the northeast border of Manongarivo, where net wooded area increased from 600m to 1200m elevation. However, the northeastern border of the reserve has historically received more human pressure because it is more accessible and is therefore home to

a larger human population (Ranaivonasy & Rakotoarisoa, 1999), and these impacts may have affected the lower-elevation results of Messmer et al. (2002). Indeed, Messmer et al. (2002) found that net wooded area subsequently decreased from 1200m to 1600m, an elevation range free of human use, suggesting that some unaccounted-for historical impact has reduced the wooded area in the low- to mid-elevation range of northeastern Manongarivo.

The point-centered-quarter analysis, though it did not produce any unique results with respect to the size of or distance between associating species, did indicate that the higher-altitude environment is more selective for which species are capable of growing to large proportions: Only four species were central species in the 1150m PCQ, compared to ten at 300m. However, the fact that three of these four species were all present in the 300m PCQ indicates that certain species, namely *Calophyllum parviflorum*, *Manilkara boivinii*, and *"Haramy"* (species unknown), are physiologically well-adapted to growing large in this ecosystem. The limited species diversity among these dominant trees at higher elevations also further supports the prestated hypothesis that the higher-altitude environment is more stressful, because only a small subset of tree species thriving at low elevation are equally strong at high elevation.

Distribution of other species across the mountainside also indicates evidence of niche-picking or species-specific environmental preferences. While some species are present at all elevations, several are limited to either low, intermediate, or high elevations. Without appropriate or verified scientific names for the majority of observed species, it is difficult to furnish information on the ideal environments for those species or to calculate any reliable diversity index. It can be noted, however, that the number of species observed does not change noticeably with elevation. Since some species, such as *E. sphaeranthum*, were observed to appear only at low elevations, whereas others such as *"Anivon"* appear only at higher elevations, the consistency in the overall species count suggests that where the preferred range of one species

ends, the preferred range of another begins, ensuring a consistent level of species diversity.

The increasing proportion of underbrush close to the forest floor (<1.5m tall) is likely the result of a change in the species or the physiology of the species comprising the understory. At lower elevations, the high underbrush (1.5-2.5m) is primarily the branches of suppressed tree saplings. These saplings, along with the high canopy closure, block sunlight and rain from reaching the forest floor and therefore prevent any growth of low-level underbrush. At high elevations, the more open canopy allows sunlight and rain to reach the forest floor, promoting the growth of low-level underbrush alongside the 1.5-2.5m saplings.

Changes in epiphyte coverage were consistent with the results of Benassi et al. (2011), with a significant increase in the percentage of moss coverage and no significant shift in percentage vine coverage. I attribute the increase in moss to higher humidity at higher altitude, which promotes the growth of highly moisture-dependent epiphytes like mosses. The lack of change in vine coverage could be due to the dependency of vines on other trees for support; with numerous small trees at high elevation and fewer large trees, there is less available habitat capable of supporting vine growth, negating the effect of more favorable climatic conditions.

No reliable source was able to provide scientific names for the two primary vine species, *ravintampiny* and *valatrohoko*, observed during this study. It was therefore not possible to further research whether the transition between these two species at 900m elevation is a result of species-specific physiological limitations that make each species suitable to a different elevation range or a result of some form of competition between the two species. However, based on the physical appearance of the species, I hypothesize that the transition is due to the decreasing canopy closure in the forest. *Ravintampiny* vines generally had thicker stems and smaller leaves than *valatrohoko*. These qualities are more suitable to a denser lowland forest where rainfall and sunlight are less likely to penetrate the canopy; suppressed plants receive little benefit from the

energy expense of creating large leaves but require an appropriate vascular system to transport the nutrients they do receive. At higher elevations, where canopy closure is lower, a larger-leafed vine like *valatrohoko* would benefit from increased access to sunlight and rainfall.

Although the primary trends observed in this study – decreasing tree size, decreasing canopy closure, increasing underbrush density, decreasing underbrush height, and increasing moss coverage – are all corroborated by previous research in other locales, several future studies are warranted to both confirm these trends on Bekolosy and to quantify or justify the reasons for them. While I here assume that the decline in diameter, height, canopy closure, and other community traits are due to the stresses associated with elevation, no climatic data was collected during this study. Knowledge of how humidity levels, average temperature, rainfall, wind intensity, and amount of sun exposure change across this elevation range throughout the year would help identify which altitude-related stresses are affecting the Bekolosy mountain ecosystem. Information on soil quality and nutrient availability would be equally valuable towards this end.

Examining how key functional traits that require long-term study change across elevation on the Bekolosy mountain chain is also important to determine if this ecosystem functions differently across elevation with respect to metrics not measured here. Previous research suggests that wood density (Swenson & Enquist, 2007), leaf size (Wright et al., 2004), sapling establishment, and tree growth rates (Cierjacks et al., 2008) should all decline with elevation but this should not be assumed; these variables may vary independently of the size characteristics measured in this study. Future studies examining whether the ecosystem shift observed by Messmer et al. (2002) at 1600m on Ansatrotro is a consistent separation line throughout the park, or if it varies based on topographical characteristics, would also help characterize the change in Manongarivo's plant community across the reserve's wide elevation range.

V. Conclusion

Consistent both with other research in Manongarivo and with research on plant communities across elevation elsewhere in the world, the plant community on Bekolosy Mountain in Manongarivo Special Reserve exhibits lower and less diverse values for key functional traits, including diameter at breast height, height of first branch, and total height, as elevation increases. In particular, there is a greater number of smaller trees, indicated by a declining net wooded area coupled with a mild increase in population density. These trends are attributed to the added stresses on plants at altitude, including wind exposure, nutrient-poor soil, and increased temperature range. However, despite decreasing canopy closure with altitude, NDVI values and total number of observed species remains the same; the Bekolosy ecosystem, at least up to the maximum altitude of 1150m reached in this study, thus remains equally productive despite the elevation change. A large portion of this productivity is due to an increase in underbrush density, including increased moss coverage, made possible by the lower canopy closure values and increased exposure to sunlight found at high elevations. Future studies addressing other key plant functional traits on Bekolosy, such as growth rates or sapling establishment, will further characterize the elevation-based shifts observed here.

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Appendix 1: Tabulated numerical values for the data presented in Figures 7 through 17

Figure	Measurement	Elevation (m)						Units
		300	500	700	850	1000	1150	
Fig. 7	Avg, Diameter (all trees)	10.36	9.59	9.27	8.75	8.21	6.66	cm
Fig. 8	(DBH ≥ 5.0cm) Min. Diameter	5.6	4.6	5.0	5.0	5.0	5.2	cm
	First Quartile Avg. Diameter	8.4	6.9	6.8	7.3	7.5	7.9	cm
	Avg. Diameter	13.3	12.9	12.9	13.4	11.4	9.7	cm
	Third Quartile Avg. Diameter	18.3	19.1	19.1	19.3	15.3	11.4	cm
	Max. Diameter	51.2	58.6	55.4	41.5	31.1	32.6	cm
	(DBH < 5.0cm) Min. Diameter	1.9	1.6	1	1.1	1.1	1.4	cm
	First Quartile Avg. Diameter	2.6	2.4	1.9	1.5	1.6	2.1	cm
	Avg. Diameter	3.7	3.0	2.6	2.3	2.4	2.9	cm
	Third Quartile Avg. Diameter	4.7	2.8	3.3	3.0	3.3	3.7	cm
	Max. Diameter	4.9	4.9	4.9	4.8	4.8	4.9	cm
Fig. 9	Avg. Height 1st Branch	6.19	2.80	5.66	4.77	2.60	3.61	m
	Avg. Total Height (all trees)	9.30	4.40	7.76	6.11	3.40	4.90	m
Fig. 10	(DBH ≥ 5.0cm) Min. Height of First Branch	1.94	2.16	0.68	1.65	0.49	0.40	m
	First Quartile Avg. Branch	4.90	3.52	8.43	9.09	2.41	5.56	m
	Avg. Height of First Branch	7.19	5.37	7.21	6.36	2.64	4.49	m
	Third Quartile Avg. Branch	9.10	7.22	10.00	8.85	2.88	7.81	m
	Max. Height of First Branch	17.27	14.21	21.17	16.04	4.37	10.29	m
	(DBH ≥ 5.0cm) Min. Total Height	4.15	3.96	3	2.06	1.89	2.2	m
	First Quartile Avg. Height	6.94	6.78	7.90	9.22	3.02	7.92	m
	Avg. Total Height	10.74	10.32	9.78	8.01	3.89	6.09	m
	Third Quartile Avg. Height	12.14	12.16	13.11	10.83	4.74	7.80	m
	Max. Total Height	21.35	22.46	23.25	20.06	10.6	14.1	m
	(DBH < 5.0cm) Min. Height of First Branch	1.1	0.8	0.56	1.01	0.28	0.51	m
	First Quartile Avg. Branch	2.92	1.46	1.63	1.63	1.31	1.80	m
	Avg. Height of First Branch	4.06	2.24	2.87	2.47	2.09	2.37	m
	Third Quartile Avg. Branch	5.19	2.97	4.13	3.56	2.25	2.93	m
	Max. Height of First Branch	6.97	3.68	6.54	6.54	3.52	5.35	m
	(DBH < 5.0cm) Min. Total Height	2.00	1.99	1.50	1.75	1.67	1.86	m
	First Quartile Avg. Height	4.02	2.43	2.55	2.54	2.27	2.72	m
	Avg. Total Height	5.99	2.84	3.68	3.47	2.56	3.45	m
	Third Quartile Avg. Height	7.32	3.25	4.78	4.40	2.84	4.17	m
	Max. Total Height	15.18	4.5	6.76	9.05	4.88	5.62	m
Fig. 11	Canopy Closure (%)	87.5	80	79.4	69	51.5	36.7	
Fig. 12	NDVI Index	0.408	0.311	0.404	0.335	0.261	0.392	
Fig. 13	Net Wooded Area	2.13	1.93	2.79	2.80	2.00	1.23	sq m
---	Population Density	0.29	0.23	0.39	0.26	0.38	0.40	trees / sq m
Fig. 14	Avg. Diameter (flat)	14.06		13.88		11.73	10.04	cm
	Avg. Diameter (steep)	11.78		11.40		10.76	9.01	cm
	Avg. Total Height (flat)	11.32		9.92		4.13	7.00	m
	Avg. Total Height (steep)	9.51		9.76		3.47	5.56	m
Fig. 15	PCQ Avg. Dist. Next Tree	0.71		0.88	1.09		0.99	m
	PCQ Avg. Dist. Next Largest	4.68		3.24	2.75		5.96	m
Fig. 17	Moss Cover (%)	0.91%	3.13%	3.32%	13.30%	18.03%	21.35%	
	Vine Cover (%)	5.48%	3.91%	8.86%	15.27%	4.10%	9.25%	