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Author

Dobbs, April M.

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FACTORS INFLUENCING EPIPHYTE HABITAT PREFERENCE IN MOOREA, FRENCH POLYNESIA

APRIL M. DOBBS

Department of Plant and Microbial Biology, University of California, Berkeley, California 94720 USA

Abstract. Epiphytes are important in forest ecosystems because they contribute to species diversity and aid in nutrient cycling. Despite this, the ecology of tropical epiphytes, particularly nonvascular species, is not well understood. This study compared epiphyte richness, cover, diversity, and species distributions to host tree diameter, canopy cover, aspect, and height on the trunk. Thirty-two *Metrosideros collina* trees were sampled for epiphyte species every 0.5 centimeters along circumferential transects at 0, 0.75, and 1.5 meters off the ground. Host tree diameter at 0.5 meters was measured, as well as canopy cover at North, South, East, and West. Epiphyte cover was lowest at the bottom of the trunk and highest at 1.5 meters. Richness correlated positively with diameter and canopy cover, but it did not vary significantly with height or aspect, according to the Wilcoxon and Tukey tests. Epiphyte cover correlated positively with canopy cover, but it did not vary significantly with diameter or aspect. Moss and fern cover increased significantly with diameter but did not vary with height. Liverwort and lichen cover were not correlated with diameter, but they were lowest at the bottom of the trunk and highest at 1.5 meters. Diversity, calculated with the Shannon-Wiener index, correlated positively with epiphyte cover and tree diameter but did not vary significantly with height. Overall, epiphytes preferred habitats in the upper trunk region on trees with high canopy cover, and their distributions were correlated with every variable except aspect.

Key words: epiphytes; habitat preference; *Metrosideros collina*; Moorea, French Polynesia;

INTRODUCTION

Epiphytes are plants that grow on trees or shrubs non-parasitically (Hietz 1998), although most "benefit substantially" from their hosts (Callaway *et al.* 2002). They can be mosses, liverworts, ferns, angiosperms, and lichens (which fungal/algal symbioses often treated as plants) (Caldiz 2005). Vascular epiphytes, which include ferns and angiosperms, alone make up 10% of the world's flora (Benzing 2001). Although little is known about nonvascular epiphytes, which include mosses, liverworts, and lichens, they contribute substantially to forest biomass and biodiversity (Holz 2003). Because epiphytes absorb much of their water and nutrients from the atmosphere, they are good indicators of air quality (Benzing 2001). They also play an important role in nutrient cycling (Nadkarni 1984).

Epiphytes have been shown to segregate along environmental gradients, especially in substrate and atmospheric moisture (Benzing 2001, Heitz 1998). For example, nonvascular

epiphytes prefer mid-montane forests with daily mist or clouds, whereas vascular epiphytes are most common at lower montane forests with less moisture (Benzing 2001). Bryophytes and lichens are particularly sensitive to moisture levels because they exhibit poikilohydry, or rapid equilibration of their internal water levels with the environment (Benzing 2001). They also require moist air to photosynthesize. Vascular epiphytes, being less poikilohydrous, can photosynthesize in drier environments. Although vascular and nonvascular epiphytes can be desiccation tolerant, or able to revive from a desiccated state, they usually thrive in moist environments (Benzing 2001). Epiphyte distribution can also vary within a constant height, due to aspect and inclination, but this is most pronounced in areas with substantial variation in light and wind levels (Kenkel *et al.* 1981).

Habitat preference in epiphytes of French Polynesia is particularly interesting because of the environmental gradients unique to islands. On Tahiti, epiphytes are common in montane

cloud forests, in which 70% of the island's endemic trees live (Meyer and Florence 1996). Such cloud forests exist on Moorea, an island near Tahiti with similar elevations. On Moorea, one montane tree species, *Metrosideros collina* Wilkes 1854, hosts more epiphyte species and has greater epiphyte cover than other trees in the same habitat (Cushing 2002). This type of environment is thought to be "among the most sensitive and vulnerable in the world to climate change" due to the specialization and endemism of its inhabitants, as well as its "steep environmental gradients" (Loope and Giambelluca 1998). Montane cloud forests have persistent and seasonal, wind-driven clouds, a high net precipitation, and increased interception of water by the canopy. These factors probably contribute to moisture and sunlight gradients by elevation and within individual trees, which causes variation in epiphyte cover.

The purpose of this study is to determine whether changes in epiphyte distributions on *M. collina* correlate with canopy cover, aspect, host tree diameter, and height on the trunk. I predict that a) epiphyte species richness and abundance will vary significantly with tree age, canopy cover, height within the tree, and aspect, b) older trees will more epiphyte cover and more species due to increased time and opportunities for succession, c) trees with the most canopy cover will have the greatest richness and cover because many epiphytes prefer moist, shady environments, and d) Richness will be lowest at the bottom of the tree due to the moisture-trapping ferns on the ground. I hypothesize that any differences due to aspect will be due to the desiccating north-to-south trade winds (Kuhlmann 1983), rather than the angle of the sun because the sun is usually overhead (Osborne 2000). My null hypotheses are a) epiphyte richness and cover will not vary significantly with tree age, canopy cover, height within the tree, and aspect, b) older trees will not have more richness and cover than younger trees, c) trees with the most canopy cover will not have the greatest richness and cover, d) richness will not decrease with increasing height.

METHODS

Site and Study Organism

All data were collected in a mid-elevation tropical forest (approximately 300 meters above sea level) called The Belvedere, in

Moorea, French Polynesia (UTM coordinates S 17° 32.434' W 149° 49.602'). My study site was a 280 meter trail connecting two North-facing lookout platforms. My study organism was *M. collina* (Myrtaceae), a tree endemic to Fiji, Samoa, Rarotonga, the Austral Islands, and Tahiti (Wright et al. 2001). One of the dominant trees at the Belvedere, it grew as a tree or shrub from 1 to 20 meters tall and had red compound inflorescences. It grew from elevations of 100 meters to mountaintops (Wickland 1999).

Experimental Design

I sampled every tree within fifteen meters of the trail, except those that forked into more than five trunks below a height of 0.5 meters. My sample size was 32 trees. Rather than measuring the diameter at the conventional 1.3 meters, I measured it at 0.5 meters because most of the trees forked just above this height. If the tree forked into two trunks below 0.5 meters, I sampled each trunk separately and combined the diameters at 0.5 meters. If a tree forked into three, four, or five trunks below 0.5 meters, I sampled the two thickest trunks and combined the diameters of all of the trunks at 0.5 meters. If a tree forked above 0.5 meters, I sampled the two thickest trunks above every fork.

I performed circumferential transects on each tree at heights of 0, 0.75, and 1.5 meters, perpendicular to the sides of the trunk. If the tree grew on a slope, I took all height measurements from the highest side of the slope. For each transect, I recorded the epiphyte species that touched the top of the measuring tape every 0.5 centimeters and estimated the directional aspect at North, South, East, and West with a compass. I estimated canopy cover at each tree by holding a densiometer (convex mirror with quarter inch grid) at arm's length (arm at 90 degree angle), facing away from the tree at its North, South, East, and West faces.

I identified the liverworts and lichens to genus and the mosses and ferns to species using identification keys by Whittier (1976), McCune and Geiser (2000), Gradstein (1989), D'Artenay et al. (in press), Piippo (1990), and Murdock and Hinkle (1999). Voucher specimens were submitted to the University of California and Jepson Herbaria, and a photograph appendix of nonvascular epiphytes was included at the end of this paper.

Statistical Analysis

I used the non-parametric Wilcoxon and Tukey Tests to compare richness, diversity, and cover with aspect, and height within the tree because my data could not be normalized, using JMP 5.1 (©2003). To test for correlations between richness, diversity, epiphyte cover, diameter, and canopy cover, I used Spearman's rho, a nonparametric version of the linear regression, also using JMP 5.1. I used Spearman's rho rather than linear regression because my data could not be normalized. To determine whether certain species preferred similar habitats, I plotted the average canopy cover and host tree diameter for each species. I calculated percent cover as the percent of occupied intervals on the transect tape divided by the total possible.

To calculate diversity, I calculated the Shannon-Wiener Index for each transect, which accounted for species richness and evenness. The Shannon-Wiener index (Rousseu, et al. 1998) was calculated as follows:

$$H = \sum_{i=1}^s [(p_i)(\log_{10} p_i)]$$

where p_i = proportion of total cover species i , and s = number of species.

To compare the four aspects, I calculated percent cover over a four centimeter band at due North, South, East, and West.

RESULTS

There were twenty-four epiphyte species total, including twelve lichen, five liverwort, four moss, and three fern species. Liverworts were on average most abundant, followed by mosses, lichens, and ferns (Fig. 1, Appendix A, B).

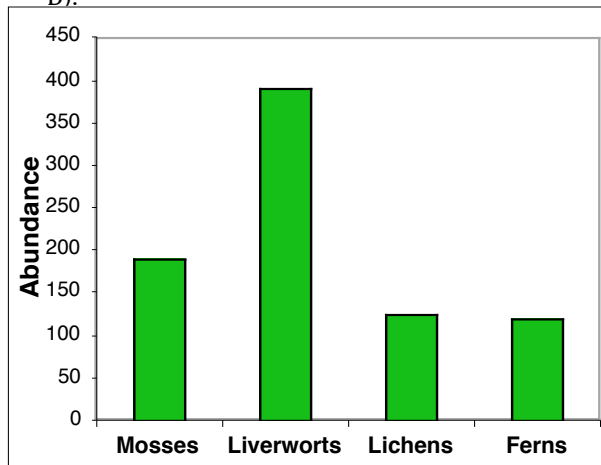


FIG. 1. Average abundance by species type

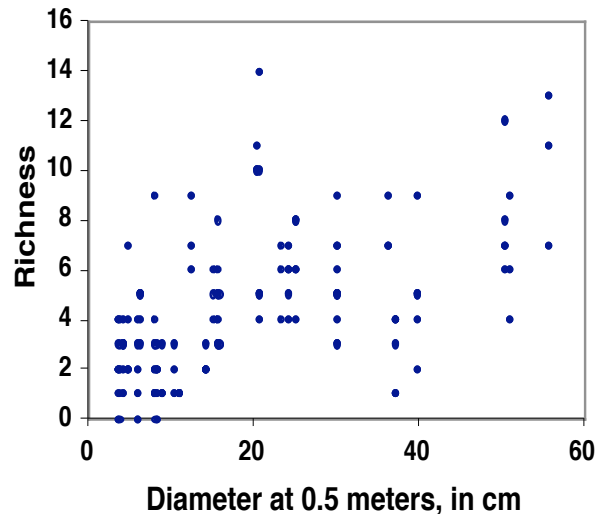


FIG. 2. Epiphyte richness by host tree

When epiphyte richness was compared among the three height groups, the three heights were not significantly different (Wilcoxon, $p=0.6861$). Richness did not vary significantly with aspect (Wilcoxon, $p=0.8540$). However, richness was positively correlated with diameter at 0.5 meters (Spearman's $\rho=0.5561$, $p<0.0001$, Fig. 2, Table 1). Richness was also positively correlated with canopy cover, although loosely (Spearman's $\rho=0.1933$, $p=0.0013$, Fig. 3, Table 1). Canopy cover was not significantly different among the four aspects.

Epiphyte cover was significantly different among the three heights (Wilcoxon, $p<0.0001$, Fig. 4, Table 2, 3). Cover was greatest 1.5 meters and least at 0 meters and was significantly different between each height (Fig. 4). It did not, however, vary with diameter (Spearman's $\rho=0.1135$, $p=0.2041$), but was positively correlated with canopy cover, although loosely (Spearman's $\rho=0.2133$, $p=0.0004$, Table 1). There was no significant difference in canopy cover among the four aspects (Wilcoxon, $p=0.4899$).

Moss cover increased significantly with diameter (Spearman's $\rho=0.4113$, $p<0.0001$, Table 1) but did not vary significantly with height (Wilcoxon, $p=0.4389$). Liverwort cover was loosely correlated with diameter (Spearman's $\rho=0.2083$, $p=0.0188$, Table 1) and increased with height (Wilcoxon, $p=0.0071$, Fig. 5, Table 2, 3). Liverwort cover was greatest at 1.5 meters and lowest at 0 meters. Lichen cover did not vary significantly with diameter (Spearman's $\rho=0.0703$, $p=0.4324$) but increased significantly

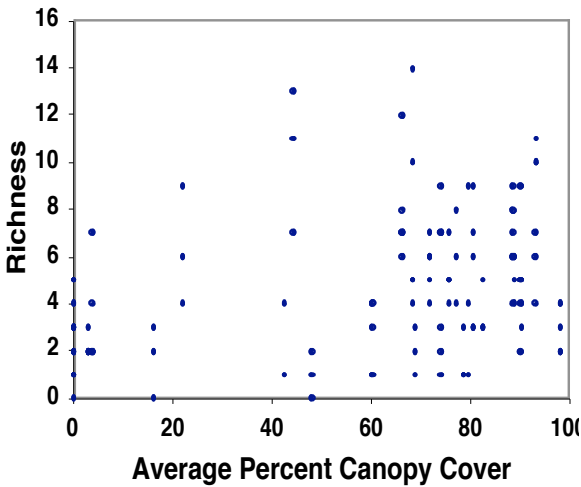


FIG. 3. Richness by average canopy cover. Although the data are not normal, an increase in richness with canopy cover is still visible.

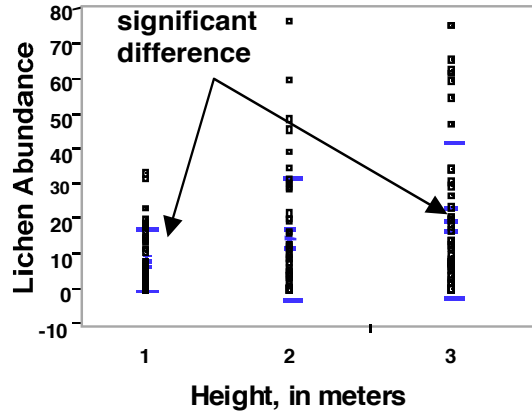


FIG. 6. Lichen abundance three heights, with means and standard deviations. Significant differences determined by the Tukey test

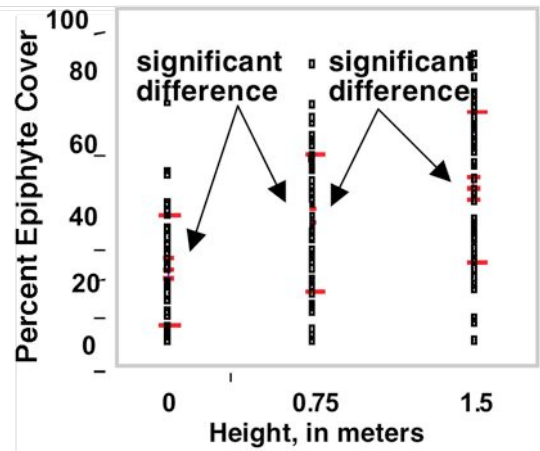


FIG. 4. Percent epiphyte cover at three heights, with means and standard deviations

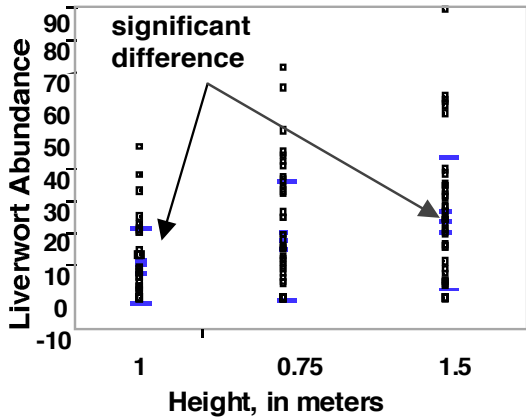


FIG. 5. Liverwort abundance at three heights, with means and standard deviations. Significant differences determined by the Tukey Test

Variable 1	Variable 2	Spearman Rho	P-value
Richness	Diameter	0.5561	<0.0001
Richness	Canopy	0.1933	0.0013
Cover	Canopy	0.2133	0.0004
Moss cover	Diameter	0.4113	<0.0001
Liver.cover	Diameter	0.2083	0.0188
Fern cover	Diameter	0.5897	<0.0001
Diversity	% cover	0.5897	<0.0001
Diversity	Diameter	0.4678	<0.0001

TABLE 1. Spearman's rho constants and P-values for significant correlations

Variable 1	Variable 2	P
Richness	Height	0.0686
Cover	Height	<0.0001
Liverwort cover	Height	0.0071
Lichen cover	Height	0.0071

TABLE 2. Wilcoxon P-values for significant correlations

H 1	H 2	Total Cover	Liverwort Cover	Lichen Cover
0.75 m	0 m	Yes	No	No
1.5 m	0.75 m	Yes	No	No
1.5 m	0 m	Yes	Yes	Yes

TABLE 3. Tukey Test pairwise comparisons of total epiphyte cover, liverwort cover, and lichen cover among the three heights within the tree. Yes=significantly different

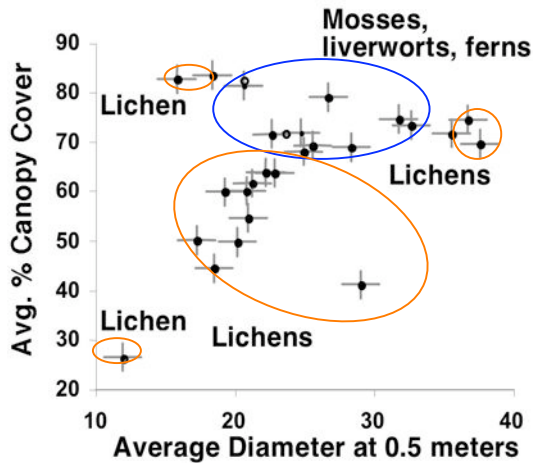


FIG. 7. Average tree diameter and canopy cover for each species, with species types circled.

with height (Wilcoxon, $p=0.0071$, Fig. 6, Table 2, 3). Lichen cover was greatest at 1.5 meters and least at 0 meters. Fern cover increased significantly with diameter (Spearman's $\rho=0.5897$, $p<0.0001$, Table 1) but did not vary significantly with height (Wilcoxon, $p=0.508$).

Epiphyte diversity, quantified by H-values, was positively correlated with total cover (Spearman's $\rho=0.3729$, $p<0.0001$, Table 1) and diameter at 0.5 meters (Spearman's $\rho=0.4678$, $p<0.0001$, Table 1). Diversity did not vary significantly with height (Wilcoxon, $p=0.3372$), which was expected because richness did not vary significantly with height.

According to the scatterplot of species distribution by average canopy cover and average tree diameter, *Lopholejeunia sp. B* and *Leucobryum tahitense* grew at the highest canopy cover levels of the liverworts and mosses, respectively, but the other liverwort and moss species grew at similar canopy cover levels (Fig. 7). All of the lichens except Lichen E, A, B, and G grew on trees with lower average canopy cover than the other species types (Fig. 7). The species were not present at statistically significant average canopy covers (Wilcoxon, $p=0.1939$), but Lichen C was at a canopy cover significant lower than the other species (Tukey Test)

DISCUSSION

The lack of variation in species richness with height within the tree supported the null hypothesis that richness would not vary with height and disproved the hypothesis that

richness would be greatest at 0 meters. It was predicted that richness would decrease with height because the *Dicranopteris* ferns covering the bottom of the tree would trap more moisture in the bark and in the atmosphere, creating an environment habitable for more epiphyte species. Based on observation, the bark under the ferns was considerably drier than the rest of the tree, presumably because the ferns intercepted rainfall and absorbed moisture from the ground. They also appeared to block most of the sunlight, creating a less habitable environment for epiphytes. Although species richness did not vary significantly with height, the drier environment at the base of the tree appeared to be inhabited more by lichens than by other species types. Because the species composition was able to change drastically without altering species richness, species composition (discussed later) was more informative about epiphyte responses to vertical environmental gradients.

The increase in richness with tree diameter supported the hypothesis that richness would vary with girth but did not necessarily support the hypothesis that older trees would have more species. Although the diameter at 0.5 meters was meant to be an index of tree age, older trees were not necessarily thicker than younger ones. Many of the thinner, shorter trees were growing in sunny areas that had been cleared for tourism. They appeared withered and unhealthy and may have had lower epiphyte richness due to other factors besides size and age. The age proxy was not reliable because of environmental variation and the fact that *Metrosideros* development in relation to diameter had not been documented. Due to the lack of growth rings in tropical trees, one would need to study multiple *Metrosideros* trees over several years to determine a precise age proxy.

Richness increased significantly with canopy cover, which supported the hypothesis that the two variables would be correlated. It also supported the hypothesis that epiphytes would prefer shadier environments rather than direct sunlight. The trees growing in sunnier areas had far less moisture in the bark (and, presumably, in the atmosphere) due to evaporation. The richness was lower on these trees probably because fewer species could tolerate the drier bark and the transpiration from their leaves. Because most of the epiphytes found were nonvascular and relied heavily on atmospheric moisture, more

species were able to tolerate shady environments due to the increased moisture and decreased transpiration. Although this conclusion is plausible, two confounding factors are a) the sunnier areas were also more disturbed, and b) the trees growing in sunnier areas seemed unhealthy or partially dead.

The total epiphyte cover was lowest at the ground and highest at 1.5 meters, which suggested a positive correlation between height and cover and supported the hypothesis that cover would vary with height. There were fewest epiphytes at the bottom of the tree, probably due to the drier environment created by *Dicranopteris*. The increase in total cover with height was primarily due to increases in lichen and liverwort abundance because there was little increase in the mosses and ferns. It is unclear whether the liverworts and lichens increased more noticeably because they were more sensitive to *Dicranopteris*, or due to another variable, is unclear. To differentiate between the two causes, one would have to study trees with and without *Dicranopteris* (controlling other variables) to see if it caused the increase in liverwort and lichen cover or magnified it. The lack of variation in fern cover was probably because ferns grew up each tree on a single rhizome with few branches. Because fern cover was recorded as basal cover, rather than foliar, the rhizomes would have had to branch considerably to cause a significant increase.

The lack of variation in total epiphyte cover with tree girth supported the null hypothesis that cover would not correlated with tree diameter. The results suggested each tree had a maximum epiphyte load within a single height that did not increase as the trees increased in girth. As each tree thickened, the spread of existing epiphytes and the introduction of new populations probably fluctuated around a carrying capacity. Because there was always some unoccupied space on the tree, the carrying capacity was probably based on moisture in the bark, rather than on surface area. Had the carrying capacity been based mostly on available surface area, the epiphytes would have covered as much of the tree as possible.

Epiphyte cover increased significantly with canopy cover, which supported the hypothesis and could be explained with similar logic as the increase in richness. As canopy cover increased, not only could more species inhabit the environment, but they could spread more quickly. While the total

cover did not change within a given height level, the richness varied within that height according to canopy cover. One problem with measuring percent cover in both wet and dry conditions was that the epiphytes were usually shriveled when dry and expanded when wet. They may have covered less surface area on trees in sunnier places because they were less hydrated, not because there were more individuals.

The scatter plot of species by mean diameter and mean canopy cover suggests segregation of some species types by canopy cover preference. The fact that all of the lichens except four grew on trees with lower average canopy cover than the other species types suggests that lichens can survive better in sunnier environments than mosses, liverworts, and ferns. The habitat preference of lichens may have less to do with desiccation tolerance than with access to sunlight, since the photosynthetic algae lived under a crusty top layer of cortex. One of the lichens appeared to prefer the least canopy cover of all of the species, which suggests that it is the most desiccation tolerant species or that it requires the most sunlight. In general, the mosses, liverworts, and ferns preferred shadier, thicker trees. The lichens appeared to grow in a wider variety of shade levels but were most likely of the four species types to inhabit sunny areas. The scatter plot, however, does not necessarily suggest epiphyte preference for tree size or shade level because all of the trees growing in sunny areas tended to be smaller than the others. In order to determine whether canopy cover, tree girth, or both caused the segregation, one would need a larger sample size that included thin trees in shady areas and thick trees in sunny areas.

The lack of variation in richness and cover with aspect supported the null hypotheses that either variable would correlate with aspect. Because canopy cover did not vary with aspect, any variation among the four aspects would have to be due to another factor besides shade level. This also explained why richness did not vary with aspect yet increased with canopy cover. The result disproved the hypothesis that the North-to-South trade winds would create a drier atmosphere on the North side of each tree. The trade winds probably had little effect on the epiphytes because most of the trees analyzed grew in densely-populated areas and were buffered from strong winds. Any trees growing in open areas, where trade

winds would have been more noticeable, were so small in diameter (less than ten centimeters) that they were not used for the aspect analysis. One problem with the part of the study was that there was a large standard deviation because the sampling area at each aspect was only four centimeters wide, and the epiphytes were sampled every 0.5 centimeters. There was also a high chance of error in determining the exact aspect with the compass. While the small sample area allowed for a larger sample size, it was not appropriate for the study.

As total epiphyte cover increased, so did the Shannon-Wiener diversity index for each transect. This was expected because richness, which comprised a major part of the diversity index, also increased with epiphyte cover. The result implied that as a tree acquired more epiphyte cover due to the spread of existing species, new species were also colonizing it. If the increase in epiphyte cover had been due mostly to the spread of existing colonies, the diversity index would not have increased at as great a rate. Diversity also increased with diameter, which coincided with the increase of richness. Just as richness did not vary with height, neither did diversity.

The epiphytes studied on *M. collina* appeared to respond most strongly to moisture, which supports the conclusions from other literature that substrate and atmospheric moisture are the greatest determining factors in epiphyte distribution. This coincided with the facts that a) epiphytes lacked true roots, and b) nonvascular epiphytes could not regulate their internal water levels as well as other plants. The most common habitat for epiphytes was the upper trunk region in thick trees with high canopy cover, which was the wettest habitat on the trunk. While this study did not measure moisture levels directly, the results suggest that moist habitats support the greatest epiphyte diversity and total cover.

Although the epiphytes on Moorea showed mostly predictable habitat preferences, they probably differed physiologically from mainland epiphytes due to their unusual environment. For example, epiphytes in cloud forests probably adapted to greater moisture fluctuations than epiphytes in temperate forests. Whether the epiphytes on Moorea and other tropical islands radiated from a few ancestors or evolved within each species, they had to adapt to new environmental pressures unique to islands. Comparative studies of habitat preferences of

mainland versus island epiphytes would illuminate differences in niche differentiation and adaptations, as well as convergent evolution among species and species types.

CONCLUSION

Liverworts, mosses, and ferns preferred shadier habitats and thicker trees than did lichens, which grew in sunnier areas but appeared to tolerate a range of shade levels. Lichens and liverworts preferred to grow higher on the trunk, but mosses and ferns did not show elevation preferences. Mosses and ferns were most abundant on larger trees, but lichen and liverwort abundances were not correlated to tree size. Epiphytes were most abundant high in the trunk and in high shade, yet were most diverse on thicker trees. Overall, nonvascular epiphyte distributions were correlated with height within the tree, canopy cover, and diameter, but were not correlated with aspect. Vascular epiphyte distributions were loosely correlated with height but were unaffected by other environmental factors. Future research should compare epiphyte populations on *M. collina* at different elevations to test wider variation in these environmental factors and determine whether epiphyte zonation by elevation occurs in remote tropical islands.

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APPENDIX A

Lichens found on *Metrosideros collina* in Moorea, French Polynesia



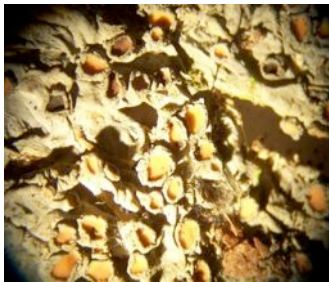
Ahtiana sp.



Ahtiana sp.



Unknown A



Melanelia sp.



Cavernularia sp.



Punctelia sp.



Unknown B



Punctelia sp.



Cavernularia sp.



Unknown C



Parmelia sp.



Cavernularia sp.

APPENDIX B

Mosses and liverworts found on *Metrosideros collina*, in Moorea, French Polynesia



Syrrhopodon banksii



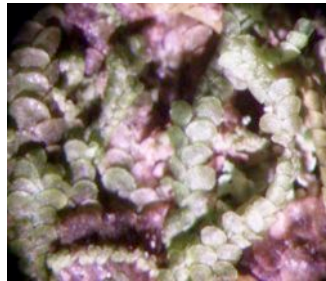
Octoblepharum albidum



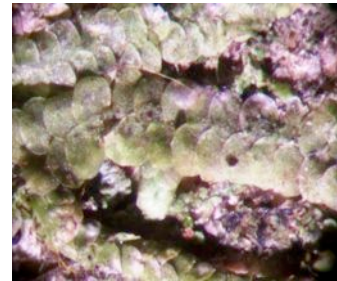
Mitthyridium obtusifolium



Leucobryum tahitense



Cheilolejeunea sp.



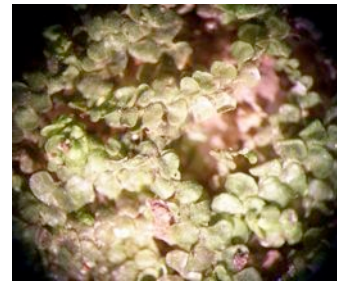
Cheilolejeunea sp.



Species unknown



Microlejeunea sp.



Lopholejeunea sp.