INTRODUCTION

Tropical rainforests are extremely important habitats, as they are some of the most biodiverse ecosystems in the world. Perhaps one of the most important features of tropical rainforests is that they store almost half of the terrestrial global carbon pool (Brown and Lugo, 1982). They provide a number of other crucial ecosystem services including evapotranspiration, temperature regulation, nutrient cycling, and water quality restoration (Edwards, 2014). It has been shown that species richness is correlated with the functioning of such services as opposed to land developed for other uses, contributing to ecosystem health and economic value for human society (Martinez et. al, 2009). Unfortunately, tropical rainforests are threatened by human induced deforestation. Tropical rainforests are most immediately threatened by habitat fragmentation as it degrades natural habitat by adding edge effects (e.g. light penetration, weed dispersal) removing canopy cover, and preventing dispersal (Edwards, 2014; Norris, 2016). Unlike many temperate species, tropical species are adapted to very specific understory conditions that are rapidly disrupted by forest clearing, and for these sensitive organisms that threatens possible extinction (Edwards, 2014). On a larger scale, deforestation allows excess carbon into the atmosphere, a major contributor to climate change right behind fossil fuel burning (Norris, 2016). Deforestation at its current rate is predicted to cause a carbon debt of 8.6 petagrams of carbon (PgC) per year and time lag effects of up to 10 years (Norris, 2016; Rosa, et. al, 2016). These changes will disrupt ecosystem equilibrium and cause a significant number of species extinctions before natural recovery is possible. With the effects of climate change in mind, efforts to conserve tropical rainforest biodiversity are important now more than ever.

Some tropical rainforest species receive more attention than others, which creates a disparity in where conservation efforts are concentrated. Bryophytes (including mosses, liverworts, and hornworts) are a very diverse group of non-vascular plants that are often overlooked. There are about 1500-2000 species of mosses and liverworts each, almost 30% of all bryophytes found in tropical rainforests alone (Gradstein and Pocs, 1989). Studies have documented bryophyte importance in regulating nutrient and hydrologic cycles as well as their role as bioindicators of atmospheric deposition and environmental...
pollution (Schuster, 1983; Shilling and Lehman, 2002; Turetsky, 2003). Filmy ferns were also considered for this study due to their abundance in epilithic communities as well as their similarity to bryophyte biology, including their ability to be extremely desiccation tolerant and capable of wide dispersal patterns (Nitta, 2006). Bryophytes make exceptional study organisms for the purposes of community ecology, as they occur in compact systems that may help better understand the complex nature of larger systems. Like many other rainforest species, bryophyte diversity is at stake due to forest fragmentation caused by land use changes in the tropics (Zartman, 2003). Focusing on their ecological roles and understanding their importance in rainforests is crucial for developing effective preservation methods for bryophytes and the species associated with them.

Some aspects of bryophyte community ecology are better studied than others. Studies have looked at communities in temperate regions with respect to community structure of epiliths, i.e., bryophytes inhabiting rock surfaces. It has been shown that local and microhabitat conditions such as surrounding tree species, bark pH, and leaf litter have significant effects on bryophyte distributions on nearby boulders (Weibull, 2001). Another aspect of microhabitat that seems to influence bryophyte community distribution is the structure of the boulders surface itself, known as microtopography. A temperate study from California demonstrated the importance of folds in the rock face that can influence how bryophytes obtain resources, and influence both large and small scale distributions (Alpert, 1986). It was further suggested by Alpert (1986), that looking at features such as slope, height, and aspect may be indicative of habitat structure that could potentially influence bryophyte distributions.

A follow up study to Weibull (2001) paper incorporated the concept of equilibrium theory, which is part of the overall theory of island biogeography (MacArthur and Wilson, 1967), to the boulders and their bryophytes. That study showed that there was a positive correlation between boulder size and species richness (Weibull and Rydin, 2005). However, it is important to note this is not a consistent finding among other studies, as some have found no distinct correlation (Kimmerer and Driscoll, 2000). It appears boulders have the potential to act as islands in providing patches of resources for species to colonize over time. The species area hypothesis, which suggests more species will populate a larger area of habitat, as well as the concept of habitat heterogeneity, stating that the more diverse an ecosystem’s productivity, the more diverse the species within, both shed light on environmental relationships that have been used to explain species distribution that may be applicable to epilithic bryophytes (Bell et al, 1994). Acknowledging the importance of these temperate studies, it is necessary to address similar studies about tropical forest bryophytes. In particular, the epilithic communities in the tropics are critically understudied.

On the island of Moorea in French Polynesia, bryophytes contribute significantly to the flora of the island’s montane rainforests. Several studies have attempted to show relationships between environmental conditions and the distributions of epiphytic and epiphyllous bryophytes, with mixed results (Fok, 2007; Parks, 2014; Kraichak, 2014). There is no current literature with regards to the dynamics of epilithic communities for the island.

The purpose of the current study was to answer the following questions with regards to epilithic bryophyte and filmy fern communities on Moorea: 1) Does community composition and alpha diversity on boulders differ based on microhabitat conditions, and if so on what scale? 2) Does epilithic taxon richness correspond to the equilibrium theory of island biogeography with respect to boulder size and boulder isolation? I hypothesized that microtopography will affect alpha diversity and percent cover on individual boulders, whereas canopy cover and plant community will affect beta diversity among sites. Additionally, taxa richness will be positively correlated with boulder size and negatively correlated with distance between boulders.

METHODS

Sample plots, boulder size, and species ID

My research took place within the Society Islands archipelago on the windward island of Moorea, French Polynesia (17.5388° S, 149.8295° W). I sampled two of the main hiking trails at the Belvedere of the Opunohu Valley, the Three Pines Pass (17° 32.096’S, 149° 49.312’W) and the Three Coconuts Pass (17° 32.841’S, 149° 50.519’W), a map detailing the location of my sites is included (Fig. 1). Along each trail, 5 plots were established at least 3m from the designated walking trail in order to avoid sampling boulders recently placed for the purpose of bordering the trail. I sampled a total of 10 plots. Plot size was selected randomly and plot size varied to ensure that at
least 5 boulders were available to sample. A minimum plot size was established as 5 x 5 meters. If within this area not enough boulders were present, the plot size was increased systematically by 1 m² and reassessed until at least 5 boulders were included in the plot. In order to ensure an adequate number of test subjects, a boulder’s dimensions for this study were defined as having a maximum length and width of at least 50 cm each, and maximum height of at least 30 cm above the ground. Common species of both bryophytes and filmy ferns were identified in lab using microscopes and in the field with ID keys.

![Image](image_url)

**FIG 1.** Map of Moorea, French Polynesia with surveyed sites marked along the Three Pines Trail (in blue) and the Three Cocos Trail (in red). Map outline obtained from QGIS software.

**Surface area, boulder isolation, and species presence**

In order to apply the theory of Island Biogeography to boulders it was necessary to approximate size of each boulder, as more species should inhabit larger boulders. I also included distance between boulders due to the role that dispersal ability plays in the theory. Species presence then would be the response factor for both the area and isolation of the boulders. Of the appropriately sized boulders in the plot, all were sampled for this part of the study (range: 5-9). The maximum length of each dimension of each boulder was recorded. From these measurements, a modified surface area for a rectangular prism was measured in cm², omitting the bottom surface, was estimated using the formula: \[2[(wh) + (lh)] + (lw)\]. Then, a presence/absence survey of the species on each boulder was assessed and it was noted if each species present was also an epiphyte or not. Then the pairwise distance of each boulder to all of the other boulders in the plot was measured in meters from the closest edge of one boulder to the closest edge of the other using a transect tape.

**Analyzing local and micro habitat and effects on distribution and diversity**

To understand factors that might influence resource availability for epilithic communities, I surveyed the available local and microhabitat. Habitat conditions measured at the per plot scale included percent canopy cover estimation and plant community assessment. Canopy cover was estimated from photographs taken and analyzed using CanopyApp. Two photos were taken from the center of the plot, and the estimations of cover for each were averaged. Plant community was assessed by counting all trees within the plot and within 1 meter of the edges of the plot, and noting each species. Tree saplings shorter than 2 meters tall were not considered for this part of the survey as they would not have contributed significantly to the canopy.

To characterize the boulders themselves, the microtopography features assessed included slope, the angle of the boulder’s surface on which species were found, height and concavity. For this part of the survey, a subset of 6 boulders were sampled randomly, such that one boulder was sampled per plot for a total of 6 plots sampled for microtopographic analysis. A point intercept analysis was conducted using a transect. For each boulder, 5 transects were laid across the surface of the boulder perpendicular to its longest dimension, either length or width. Species presence was recorded along each transect at 5 cm intervals, starting from the base at one end and ending at the base on the opposite side. If no species were present at a point, it was not considered for this part of the survey as they would not have contributed significantly to the canopy.

Borrowing from and modifying the methods of Alpert, 1986, slope was recorded on a 5 cm scale, for each valid point along each transect. The approximate angle of the slope was found using a level, on which 5cm length was marked, creating a right angle with an opposite angle side length, and then using trigonometry to solve for the angle of the slope. Slope ranged between 0 to 90 degrees. Height was measured for each valid point by measuring each point’s distance from the ground in centimeters. Due to the complex surface structure of the boulders, features of concavity were categorized to note the types of surfaces on which species may habitually occur. The following categories of concavity were
qualitatively established: flat, a surface which is smooth with no changes in elevation; concave, where the surface inclines to a peak that is either rounded or sharp; and convex, where the surface creates a crevice or pocket that is either rounded or sharp.

**STATISTICAL ANALYSIS**

*Surface area, distance between boulders, and species presence*

According to the Theory of Island Biogeography, habitat size is positively correlated with species richness. To test this part of that theory I regressed species richness against surface area (cm²) of each boulder. The second part of the theory expects a negative correlation between distance and species richness, therefore I also regressed species richness against mean pairwise distances (m) for all boulders. The alpha value was set to .05 in the above regression analyses.

*Analyzing local and micro habitat and effects on distribution and diversity*

I hypothesized that local habitat conditions of canopy cover and surrounding plant community would harbor significant effects on richness for my sites. To interpret a possible relationship for canopy cover, average species richness per site was regressed against average canopy cover estimates (%) per site. Similarly, for plant community average species richness per site was regressed against percent *Inocarpus fagi fer* dominance per site, since this species was the most prominent throughout sites in general. Again, alpha was set to a significance value of .05.

For microhabitat analysis, the values for slope (0-90 degrees) and height (cm) for the entire subset of boulders were summarized in box plots to show common habituation trends for slope and height of each species. For both, an ANOVA test was conducted to test for significance followed by a Tukey test to investigate significant differences in these counts among species pairs. The most frequently occurring species were considered when analyzing the Tukey test results. Similarly, the counts for concavity preferences for all species were summarized and compared to one another. A chi-squared test was used to test for significant variation among species. For each of these parameters, a significance level was also set at .05.

Alpha diversity was used to quantify local diversity trends. Each boulder was surveyed using Simpson’s Diversity Index, calculated as: \[ D = \sum (n / N)^2 \]. Here n is the number of specific species and N is the number of total species.

For this index values range from 0-1, 0 being the most diverse, 1 being the least. These values were then averaged for each site. Then ANOVA test was used to look for significant among these averages. Since boulders were theorized to share the same role as islands do in the Theory of Island Biogeography, beta diversity was the metric used to compare turnover rate of diversity in relation to distance between boulders at each site. To do this Sorensen’s Index of dissimilarity was used, with values ranging from 0-1 as well, where 0 indicates dissimilarity among sites and 1 indicates complete similarity. All pairwise combinations of boulders across sites were compared and an average value was taken. These two scales of diversity were used to see how diversity differed within and among sites. The significance level was set at .05 for each.

In order to show the degree to which all sites, boulders, and species are ecologically related, a non-metric multi dimensional scaling (NMDS) ordination was constructed using R statistical software and included. The NMDS ordination treated all sites as different communities when comparing them, and did the same when comparing species. Ecological distinction between groups is determined based on the degree of separation among the communities. More distance between 2 groups means they are more ecologically distant as well.

**RESULTS**

For this study, boulder surface area ranged from 11,236 cm²-203,391 cm² in size. Average pairwise distances between boulders ranged from 0.9m-4.7m. I documented a total of 13 species of bryophytes and filmy ferns (Appendix A) on the boulders I surveyed. Bryophytes included 8 species of mosses identified to species: *C. tenerum*, *E. solanden*, *F. mangarevensis*, *I. albescens*, *N. lepineana*, *O. cylindricum*, *O. rugosipes*, and *V. aperta*; as well as 3 species of liverwort identified to family: *Lejuneacea sp. 1, Lejuneacea sp. 2, and Phlagiochila sp.*. Filmy ferns included 2 species of *Crepidomanes: C. bipunctatum and C. humile*. Of the species identified 6 were considered the most commonly observed including *F. mangarevensis*, *I. albescens*, *Lejeuneacea sp. 1, Lejeuneacea sp. 2, C. humile and C. bipunctatum*. The most species found on a single boulder was 12, the least was 3. For local habitat conditions the range of canopy cover estimates per site was between 48.82% to 66.73% and *Inocarpus* dominance had a wide
range of percentages (0-100%). Average species richness per site ranged from 5-10.4.

Surface area, boulder isolation, and species presence

The applicability of the Theory of Island Biogeography to boulders relies on the relationship of boulder size and isolation to the richness of species found for this study. The linear regression of species richness by boulder surface area (FIG. 2) was found to be statistically significant and positively correlated (P < .05, P = .0006837).

FIG. 2 Linear regression showing the correlation between boulder surface area and species richness for each boulder surveyed (P-value = .0006837). Shaded area represents standard error.

Next, the regression of species richness by mean pairwise distance (FIG 3.) to determine influence of boulder isolation was not statistically significant (P > .05).

FIG 3. Linear regression displaying the relationship between individual mean pairwise distances and species richness for each boulder (P-value = .7223). Shaded area represents standard error.

Analyzing local and micro habitat and effects on distribution and diversity

Using canopy cover and plant community as parameters to determine local habitat conditions yielded the following results. The regression of average species richness by average canopy cover (FIG. 4) were not correlated and therefore not statistically significant (P > .05).

FIG. 4 Linear regression showing the relationship between average percentage canopy cover and average species richness per plot (P-value = .3784). Shaded area indicates standard error.

Similarly, the regression of average species richness by percentage Inocarpus fagifer dominance (FIG. 5) was not significant (P > .05).

FIG. 5 Linear regression between plant community composition, measured as percent Inocarpus fagifer dominance, and average species richness per plot (P-value = .5583. Shaded area represents standard error.
Slope, height, and concavity counts were analyzed for micro habitat and results served as a comparison of these parameters amongst all species. The results of the ANOVA test for species slope occupation (FIG 6.) was statistically significant (P > .05). Next, the Tukey test results showed specific significant differences between several pairs of species. Due to their dominance throughout this study, the pairs including 6 most common species are considered for this portion of the results. Statistical significance was found for the following pairs: I. albescens-C. bipunctatum, Lejeuneacea sp. 2-C. bipunctatum, I. albescens-C. humile, Lejeuneacea sp. 2-C. humile, I. albescens-F. mangarevensis, Lejeuneacea sp. 2-F. mangarevensis, Lejeuneacea sp. 1-F. mangarevensis. (P < .05).

ANOVA results for height frequencies amongst species (FIG. 7) were also found to be statistically significant. A Tukey test also was able to find significant differences between the following pairs of the 6 most common species: Lejeuneacea sp. 2-C. bipunctatum, Lejeuneacea sp. 2-C. Humile, I. albescens-F. mangarevensis, Lejeuneacea sp. 2-F. mangarevensis, Lejeuneacea sp. 1-I. albescens, Lejeuneacea sp1.-Lejeuneacea sp. 2 (P <.05). Lastly, the chi-square test for concavity preferences among species (FIG. 8) revealed statistically significant differences between species (P <.05, P = .0001983).

FIG 6. Boxplot showing the slope of a boulder’s surface upon which each surveyed species is most commonly found. Here all species are compared (P-value <.05). Slope ranges from 0-90 degrees. Bold vertical line represents mean slope value, interquartile range shown as box, horizontal lines denote variance, and black dots indicate outliers.

FIG 7. Boxplot showing the height from the ground in centimeters that each surveyed species was found (P-value <.05). Here all species are compared. Bold vertical line represents mean slope value, interquartile range shown as box, horizontal lines denote variance, and black dots indicate outliers.

FIG 8. Barplot indicating the category of concavity for which a species occurs on a boulder (P-value <.05). Here all species surveyed are compared. Concavity was separated into three categories: concave (CV), in pink; convex (CX) in green; and flat (F), in blue.

Given that canopy cover and percent cover were not statistically significant parameters, they were not used in determining alpha and beta diversity indices for this study. Instead the results for alpha diversity from the Simpson’s Diversity Index (FIG 9.) for all boulders were averaged among sites and compared.
An ANOVA test revealed that the averages were not significantly different (P < .05). For beta diversity, the Sorensen’s Dissimilarity index (FIG 10.) values were averaged and the means was .3655.

The NMDS ordination (FIG. 11) for all 10 of the surveyed sites reveals ecological differences between per site community structure and among species individually. Overall, most sites overlap one another. Cocos site 3 and 4 show almost no overlap with other sites, their greatest distance is from Pines 1, they also share overlap with each other. The remaining sites all share overlap to varying degrees, most notably all of the Pines sites. Cocos site 2 has the greatest overlap with the Pines sites compared to the rest of the Cocos sites. The distances between individual boulders, represented as numbers, within the same site overall are short. Some distances such as point 3 and point 19 for Pines site 1 and Pines site 4 respectively, vary greatly within their own site. Species ecological distances are also shown with the species names in red. The most similar species to one another are *Phalgiochila* sp. and *V. aperta*, as well as *I. albescens* and *F. mangarevensis*. All other species show greater distances from each other.

**DISCUSSION**

**Surface area, boulder isolation, and species presence**

There was a significant positive correlation between boulder size and species richness. This
result supports the hypothesis proposed by the Theory of Island Biogeography that island size, or habitat size, is positively correlated to colonization rate by more species (MacArthur and Wilson, 1967). This result for my study agrees with the findings of Weibull and Rydin (2005). However, these results were not found to be consistent among another aforementioned study by Kimmerer and Driscoll (2000). Among the two studies, each were conducted in very similar temperate regions, however, the latter worked with fewer bryophyte species. Kimmerer and Driscoll found a similar amount of species as my study found, 19 and 13 respectively. Usually, less species present in a given region reduces the chances of seeing significant variation in richness regardless of boulder size (Weibull, 2005). This may have played a part in why Kimmerer and Driscoll (2000) did not find a significant relationship. However, having found a sparse amount of species for my study, it seems counterintuitive as to why I was able to confirm a relationship between boulder size and species richness.

Results have indicated that boulder isolation within a site has no significant relationship to species richness. Theoretically, MacArthur and Wilson (1967) quantify isolation in relation to how far away an island is from the mainland, as the main pool of species that could possibly disperse across islands. This portion of the theory was not applicable to my study because of the nature of boulders themselves, as there simply is no mainland to relate distance to. Therefore, one idea that I did not consider for this study was how to quantify the degree of isolation. This is important considering most species encountered were also epiphytes. Due to the high dispersal ability of bryophytes and filmy ferns, many of the nearby trees with these similar communities is a factor that confounds true isolation of any of the boulders I sampled. To conclude speculations in relation to Kimmerer and Driscoll’s (2000) lack of variation in species diversity at their sites, this previously unmentioned factor could play a role. It is possible that since there was such a large species overlap between epiphytic and epilithic communities at my sites, that it was easier for more species to cross inhabit the boulders as well as the nearby tree species. Their sites may have very different communities and lower chances of cross inhabiting both trees and boulders.

Analyzing local and micro habitat and effects on distribution and diversity

Canopy cover and the surrounding plant community have no significant effect on average species richness among sites as indicated by the results. However, in other studies these factors are shown to have had significant influences on bryophyte distributions (Dobbs, 2006; Weibull, 2001). Considering how the survey was conducted, each regression only considered data for the sites themselves. This could be too little information to develop a significant pattern that might be more telling of the influence that these two parameters might have on epilithic communities. Canopy cover may be important to consider in future studies on a per boulder scale as opposed to site scale due to the fact that micro distributions of species are better understood when analyzed on more appropriately sized scales (Alpert, 1986). Nearby plant community has also been known to influence epilithic bryophyte community structure because of biological and chemical cycles that connect the two (Weibull, 2001). For future studies and to better understand the potential of influences of surrounding tree species it may be important to categorize stand characteristics in a way that attempts to include the diversity of tree species, as my results simplified the community down to only I. fagifer dominance. It is likely that different tree species may have specific means of influence based on their biology and ecological relationship to their surroundings. Other local habitat factors have been considered in other studies for epiphytes such a humidity, temperature, and influence of edge effects, which may be necessary to consider for epilithic communities to see if a significant relationship can be determined and the scale at which that is possible (Fok, 2007; Kraichak, 2014).

The most significant results have revealed the influence of microhabitat on how these bryophyte and filmy ferns communities are distributed. Slope and height specifically had the strongest relationship among species, concavity was not as strong but was still significant. These results suggest the importance of microtopography on boulders influencing micro distributions. Looking at these parameters, the way certain species distribute themselves can be explained by physiological limitations of each individual species (Alpert, 1986). Resource availability is also highly linked to physiological limitations and further coincides with the results. For future studies it is necessary to consider not species biology, but also how they interact within the communities themselves. Phylogenetic analysis may also help explain
how these species interact with one another and the environment based on their genetics and evolutionary relationships.

The results for diversity cannot be attributed strongly to local habitat factors due to the insignificant relationships shown in the results for local community influence. Alpha diversity values were not significantly different within the sites themselves as the averages showed. This means that within a plot, species richness did not vary greatly among boulders. However, the average beta diversity, which describes the turn over diversity among sites was relatively low, indicating dissimilarity among the sites. Ultimately, this means diversity was greater among sites than within the sites themselves. The NMDS ordination shows very little ecological differences among sites as they overlap strongly. Sites also have similar community structure due to the fact that very few species were found in the survey, which is just the nature of the region.

In conclusion, this study reveals important ecological information that can be used to further expand on more effective conservation strategies for tropical bryophyte and filmy fern communities. These species are crucial when considering plant diversity in general in these tropical regions.

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APPENDIX A

A catalogue of all bryophyte and Filmy Fern species found for this survey. All photos were taken through either a dissecting or light microscope.

I. Bryophytes
   i. Mosses

<table>
<thead>
<tr>
<th>Calymprese tenerum</th>
<th>Entodon solanden</th>
<th>Fissidens mangarevensis</th>
<th>Isopterygium albescens</th>
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</thead>
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<td><img src="Entodon_solanden.png" alt="Image" /></td>
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<td><img src="Isopterygium_albescens.png" alt="Image" /></td>
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<td>Orthorrhynchium cylindricum</td>
<td>Oxyrrhynchium rugosipes</td>
<td>Vesicularia aperta</td>
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ii. Liverworts

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II. Filmy Ferns

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