

Epiphytic Community Composition, Zonation, and Succession on Tahitian Chestnut (*Inocarpus fagifer*) Bark

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Abstract. Communities of non-vascular plants, vascular plants and lichens comprise epiphytic communities found on *Inocarpus fagifer*. This study explored how these communities are structured at two different sites on the island of Moorea, French Polynesia and compared the abiotic conditions between these two sites. The sites differed in terms of temperature ranges and humidity. Multivariate analysis revealed that these differences had a significant effect on the communities. The data was subset by site and analyzed again to see how the community was structured with distance from the apical bud which served as a proxy for age. By using the bark of *I. fagifer* as a chronosequence this study revealed that community composition does change with respect to age. The data suggested that divergent succession is occurring within each epiphyte community. In addition it was shown that species richness is correlated with total epiphyte cover suggesting a possible facilitation mechanism behind the succession. This study contributed to our understanding of community dynamics in a small rain forest ecosystem and will help serve as a starting point to begin unraveling the complex interactions that have very real implications for conservation efforts.

Key words: *Succession, community ecology, bryophytes, epiphytes, chronosequences, poikilohydrates, French Polynesia.*

INTRODUCTION

Community ecology is a subfield within biology that concerns itself with assemblages of organisms living together and the abiotic conditions they inhabit. This field has many practical applications as well as theoretical implications, even when studying a single species, as community interactions may be one of the most important factors influencing its biology (Gauch 1982). In addition to studying these communities across space, studying them across temporal scales can uncover succession and successional mechanisms.

Successional patterns have been noted in community ecology since 1860, when Thoreau set out to study species successions that occur after trees are cut down (Thoreau 1860). The study of ecological succession has since evolved from philosophical inference to quantifiable hard science and has played an integral role in understanding plant communities (Ellis & Ellis 2013). Connell and Slatyer give a useful definition of succession in their 1977 study: "Succession refers to the changes observed in an ecological community following a perturbation that opens up a relatively large space" (Connell & Slatyer 1977). Worldwide ecosystems are being disturbed at a rate of approximately 5-7 million ha per year (Wali 1999). A fundamental knowledge of

both how these communities are structured according to abiotic factors and how they change through time will play a key role in guiding rehabilitation and conservation efforts.

Succession is generally divided into two types. Autogenic succession occurs when changing biotic conditions in the environment cause a change in community structure. Allogenic succession occurs when changing abiotic conditions causes the community change (Stone 1989).

Many models of succession are constrained by the very slow replacement of species and the inability to look back in time to see what preceded them. In this regard chronosequences, or ecological units with similar characteristics but different ages, are invaluable (Kraichak 2013). Trees host multiple chronosequences: their leaves and their bark. In addition to their chronosequences trees are fruitful study subjects for community succession as they are relatively stand alone ecological units that display marked differences from their surrounding substrates, giving them the 'island' qualities of a model system (Southwood & Kennedy 1983). In addition trees have the added peculiarity of being a living and growing ecological unit. This is useful in succession because there is

constantly new bark and leaves being created which is free of propagules. Trees grow from the apical bud making it easy to identify relative age of the bark even when absolute age cannot be determined. Thus the present study uses distance from the apical bud as a proxy for relative age as bark higher on a tree will always be younger than the bark below it.

Growing on these chronosequences are epiphytes, or plants that live on other plants. Epiphyte communities are composed of mosses, liverworts, lichens and vascular plants. Bryophytes (mosses and liverworts) and lichens are well suited to studies of community ecology because of their non-vascular nature, which makes them poikilohydrates. Poikilohydrates are organisms that equilibrate their internal water content to the external environment; this poikilohydry makes the epiphyte community particularly sensitive to abiotic conditions like humidity (Mishler 2003). Mishler also notes that poikilohydrates are essentially social organisms that interact through water conduction and potentially pheromone signals. Thus its poikilohydry makes this community especially sensitive to both spatial and temporal changes.

Many studies have been conducted on epiphytic communities in terms of dispersal and eco-physiology but in terms of distribution and diversity they are understudied, particularly within the Southern Hemisphere (Burns and Dawson 2005).

The island of Moorea in French Polynesia has been the site of several epiphyte studies, which have largely looked at abiotic factors influencing community composition, richness and distribution. One study found richness to be correlated with tree diameter and canopy cover (Dobbs 2006). Another study found differences in species composition at different elevations and also found differences among different heights within a single tree, which was interestingly attributed to a micro-climatic gradient and not investigated further (Dobrowski 1996). A third epiphyte study tested the differences between epiphyte communities on six different tree hosts and tested their various abiotic factors such as water retention capacity and bark pH but found they were not significantly different between tree species (Cushing 2002). Cushing furthermore was able to make a strong suggestion that there could be more than substrate preference influencing community composition. She suggested that

there might be ecological and biotic components intrinsic to the communities that could contribute to the community composition.

I applied similar techniques within a single tree species to make inferences as to whether there was a successional signal in the data. Additionally I compared epiphyte communities of a single host tree species at different locations to see if abiotic factors structure the communities. For my host tree species I chose *Inocarpus fagifer*, (or Tahitian Chestnut) because of its widespread distribution and abundance of saplings. Tahitian Chestnut is a Polynesian introduced tree found widely throughout the islands of the Pacific. It is a tropical evergreen of the legume family and is prevalent in a multitude of Moorean ecosystems (Pauku, R.L. 2006). The study location makes the epiphyte communities of these trees particularly relevant: the rate of rain forest disruption is approximately 25 ha per year, or 5 times the global average of ecosystem disruption (Wali 1999). As epiphytes comprise upwards of 10% of rain forest biodiversity and contribute to nutrient cycling (thus affecting the larger island ecosystem at a whole) understanding their ecology is of utmost importance for rainforest conservation efforts (Nieder et al. 2001).

In the present study I explored how the corticolous (bark living) epiphyte community composition differs between two different sites and looked to see if there were climatic differences that could account for such differences. Within each site I studied how the community differed with respect to distance from the apical bud, which was used as a proxy for age. In order to make inference about possible mechanisms behind successional data I recorded species richness and total epiphyte cover for every tree section surveyed and ran a series of interspecific interaction tests in the laboratory. I hypothesized that: (1) there will be considerable differences in community structure between sites reflecting differences in the abiotic conditions, (2) that in each site communities will change consistently and significantly across time and (3) that species richness and total cover will be positively correlated and that the experimental tests will reveal significant species interactions. Thus my overall goal was to test whether or not there are distinct communities along the length of the tree. In addition by testing for facilitation/hindrance interactions and abiotic

changes I aimed to reveal possible autogenic or allogenic successional mechanisms.

METHODS

Epiphyte Collection and Identification:

The study took place on the Island of Moorea [Fig. 1] on French Polynesia at 2 sites: site 1 was on Mari Mari Kellum's property (Fig.1, point 1: -17.5135, -149.8453), and site 2 was at the Oponohu stream crossing (Fig 1, point 2: -17.5325, -149.8389) slightly further inland. Both sites were chosen for their accessibility and their abundance of *I. fagifer*. The experimental portion of the study was done at the Gump field station laboratories.

I surveyed *I. fagifer* saplings from both sites to create photo references for the epiphytes (see appendix A). Species identification was performed with microscopy to the species level where possible, with decreasing taxonomic resolution where my expertise was lacking or where there was no species name (as was the case for many lichens). I used various keys for identification purposes (Whittier 1976, Gradstein 1989) and confirmed these with Professor Brent Mishler and Bier Kraichak. Vouchers of each species were deposited in the University and Jepson Herbaria at UC Berkeley.

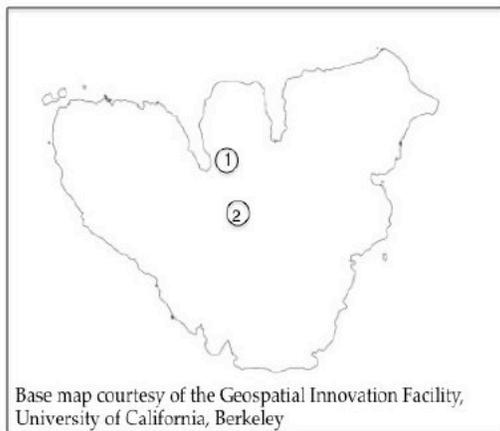


FIG. 1. Study sites on Moorea, French Polynesia

Abiotic Conditions

Climatic data such as temperature, humidity and canopy cover were collected at each site in order to quantify how they differed abiotically. Temperature and humidity were recorded at each site using a

Hoboware© data logger which took readings every 5 minutes over a 5 day period. The daily means and ranges for temperature and humidity were recorded. I then used R software and conducted a t-test on the daily means and ranges of the two sites to find the differences between the locations (All analyses were conducted in R: R Development Core Team 2013). Canopy cover was measured twice at each site: for each measurement I picked 12 random locations within each plot and quantified canopy cover using a densitometer. I then performed a Wilcoxon signed rank test on the data with respect to site (data was not normal).

Field Surveys

Sampling was performed over a 1.5-month period from the middle of October to the end of November. At each site I searched for a plot with an adequate density of replicates (saplings from 100-300 cm in height) and chose a random tree within that plot. I subsequently expanded my radius outward, sampling every tree eligible, until I had 21 trees sampled per site (each site was had a diameter of approximately 30m).

At the base of each tree I tied a string around the trunk and spiraled it up to the apical bud. Starting at 0-10 cm from the apical bud I performed a line transect randomizing for orientation by placing the transect line parallel to the trunk wherever the pre-chosen distance from the apical bud crossed the string spiral. I counted the proportion of each epiphyte seen in regards to the overall cover using a ruler. Where species were not easily identifiable with a hand lens they were carefully scraped off and pressed in paper to be taken back for microscopy analysis. Individual species cover and total cover were measured for each transect (some specimens were clearly on top of one another therefore proportions may add to more than 1). This sampling was repeated every other ten centimeter transect (0-10cm, 20-30cm etc.) until the base of each tree.

Interspecific Interactions

In order to test interactions between species I performed a DeWitt's replacement series based on an approach used by Wu (2012). Two specimens of bryophytes were picked based on field observations (each was more prevalent in a different site and they were often seen growing over each other). 20

mg of *Lophocolea subfusca* and 20 mg of *Orthorrhynchium sp.* were chopped separately using a razor blade until they had a particulate consistency. Each was subsequently mixed with 10 ml of water to create bryophyte paint. They were then painted onto filter paper and placed within a petri dish for growth (Fig. 2). 4 petri dishes had singular mosses to assess independent growth rates (2 each), 2 petri dishes had the mosses in a 1:1 mixture adjacent to each other, 2 petri dishes had a mixture of 2:1 *L. subfusca* to *Orthorrhynchium sp.* respectively, and 2 more had a mixture of 2:1 *Orthorrhynchium sp.* to *L. subfusca* respectively (sample number limitations were due to the availability of petri dishes in a remote setting). Each plate was painted on 4 November 2013 and photographed every week for 4 weeks. Each photograph was then analyzed in Photoshop to determine if there was any growth, determined from changes in surface area.

Additionally I plotted species richness and total epiphyte cover for each transect and performed a Spearman correlation test using total cover as the response variable.

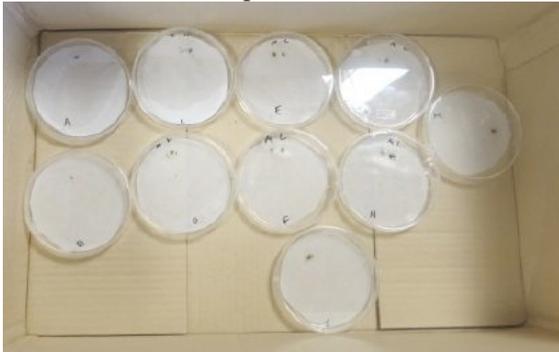


FIG. 2. DeWitt's Replacement Series

Testing for Community Differences

Community composition was quantified using proportion of the transect covered. To gauge how communities differ from one another I used a multivariate approach creating an N-dimensional space to describe the communities with each dimension being the proportion of the transect the species occupied. I ran a principle components analysis (PCA) on all the data in order collapse N-dimensions into 2 axes to visualize the community differences between sites. I used a multivariate analysis of variance (MANOVA) on the community data using study site as a categorical independent variable.

I then subset the data based on site and ran a separate PCA for each subset throwing out species if they weren't found at that site in each (to avoid an error brought about by having a constant value for an entire column). I then tested for the Spearman correlation (as PCA score 1 was non-normal) between PCA score 1 (the score that highlights the largest amount of difference in the community data) and distance from the apical bud. I performed two more MANOVAs, this time using categories based on different distances from the apical bud as the independent variable.

RESULTS

Abiotic Variation Between Sites

Average daily temperature was not significantly different between sites ($P=0.11$). Site 2 was more humid than site 1 [Fig 3] with percent humidity's of 92.5 and 87.75 respectively ($P=0.005$). The daily humidity range between sites was not significantly different between sites ($P=0.65$). Site 2 had a greater daily range in temperature than Site 1 [Table 1] with a ranges of 8.32 and 6.06 Fahrenheit respectively ($P=0.047$). Canopy cover between the two sites was not significantly different ($P=0.09$)[Fig 4].

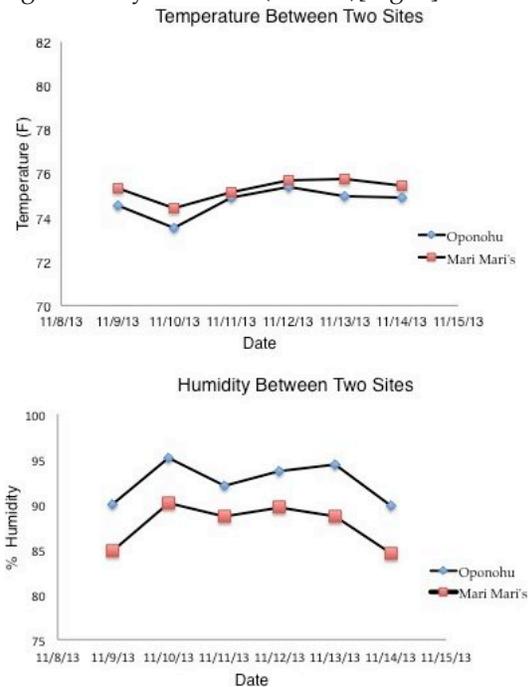


FIG. 3: Average Temperature and humidity between sites

TABLE 1. Daily ranges in temperature and humidity

Date	Mari Mari's Humidity Range	Oponohu Humidity Range	Mari Mari's Temp. Range	Oponohu Temp. Range
11/9/13	11.01	23.32	5.73	9.06
11/10/13	13.91	10.71	3.63	7.82
11/11/13	18.46	14.32	7.13	7.64
11/12/13	16.11	16.32	6.62	9.22
11/13/13	14.15	13.48	4.7	5.58
11/14/13	18.87	20.92	8.52	10.61
	Mean:15.42	Mean:16.51	Mean:6.06	Mean:8.32

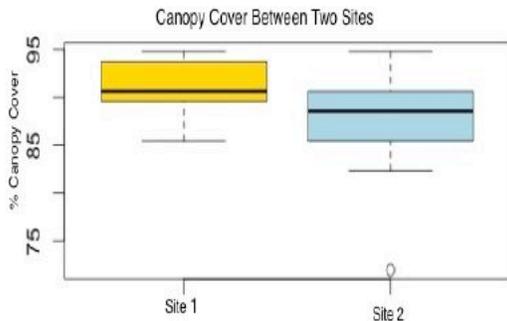


FIG. 4. Canopy Cover Boxplot

Community Differences:

The PCA graph was color coded by site and allows for visualization of the community compositional differences between the two sites [Fig. 5]. A multivariate analysis of the communities showed that site had a significant effect on the community composition (MANOVA: $F=9.14, d.f.=389, P=1.54 \times 10^{-11}$).

Site 1's PCA score 1 was shown to be significantly correlated with distance from the apical bud (Spearman: $r=-0.52, P=1.84 \times 10^{-15}$) [Fig. 7]. Site 2's PCA score was also shown to be significantly correlated with distance from the apical bud (Spearman: $r=-0.62, P=2.2 \times 10^{-16}$) [Fig. 7]. The multivariate analysis of variance for site 1 showed that distance from the apical bud had a significant effect on the community composition (MANOVA: $F=14.11, d.f.=153, P=2.86 \times 10^{-15}$). Similarly the multivariate analysis of variance for site 2 showed that distance from the apical bud had a significant effect on the community composition (MANOVA: $F=17.6, d.f.=152, P=9.86 \times 10^{-14}$).

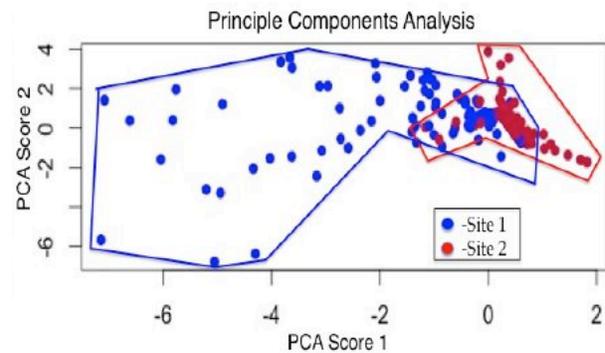


FIG. 5. Principle Components Analysis showing differences in community structure.

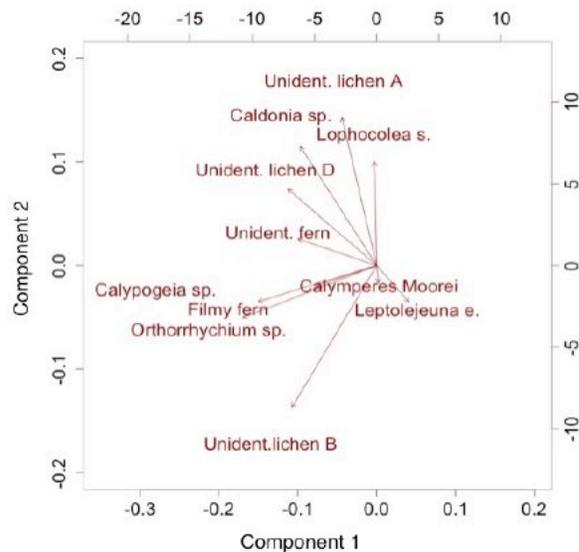


FIG. 6. Bi-plot of the PCA weighted to show which species comprise most of the variance seen between points.

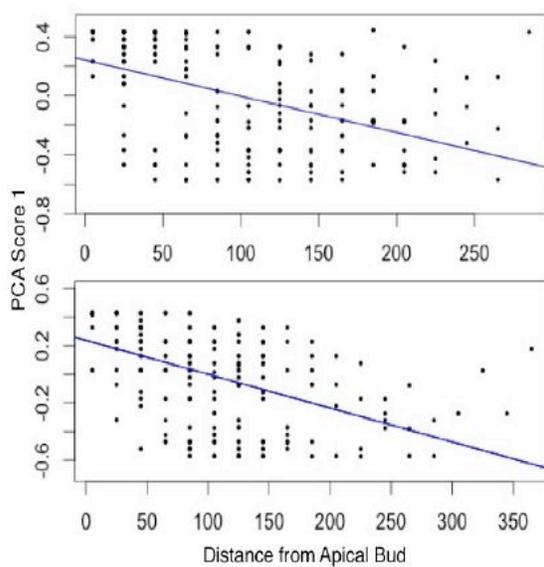


FIG. 7. PCA score 1 was plotted against distance from the apical bud for each site separately. (Site 1: top. Site 2: bottom.)

Interspecific Interactions:

During the four-week growth period neither bryophyte in any proportion changed in regards to surface area when analyzed in Photoshop, therefore no further statistical tests were performed.

A Spearman's rank correlation showed that species richness had a significant positive correlation with total epiphyte cover (Spearman: $r=0.75, P=2.2 \times 10^{-16}$) [Fig. 8].

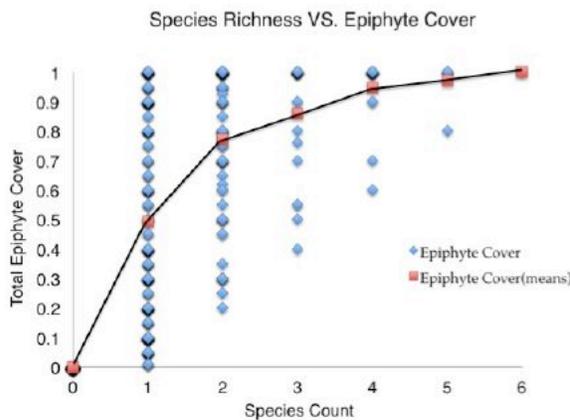


FIG. 8. Total epiphyte cover in relation to species count, the means of cover for each richness level was plotted in red to show a possible logarithmic relation.

In other words as the number of species on a segment of bark goes up there will tend to be an increase in the total amount of bark that is covered by epiphytes.

DISCUSSION

Variation Between Sites

Site 2 is more humid than site 1 on average; additionally it experiences a larger daily range in temperature [Fig 3, Table 1]. These differences can have a large impact on the epiphytic community. Bryophytes and lichens are small in size and lack a vascular system, which puts them in intimate contact with their micro-environment and makes them sensitive to climatic changes (Mishler 2003). The MANOVA showed that location had a significant effect on the community. This can be visualized in my PCA [Fig. 5], which shows that the communities of each site occupy slightly overlapping yet distinct portions of multi-dimensional space in which each dimension is based on the abundance of a particular species. The PCA biplot [Fig. 7] shows which species are comprising most of the variance seen in the in the PCA plot [Fig. 6]. Species with longer vector lengths are accounting for more of the variance seen in the component axes they are parallel with and thus for more of the variance in community composition. For example the bi-plot vector for unidentified lichen B suggests that the communities on the lower left side of the PCA plot have unidentified lichen B present in them. The points on this portion of the plot are all also from Site 2 meaning 'Unidentified lichen B' is a good indicator species for the community at that site.

Microclimate is a factor that structures these biological communities and cannot be overlooked when comparing the communities across other factors like age as it might confound that analysis. Future studies would benefit by looking at how small these microclimates could be before they stop having an effect on the community. This data would allow for analysis of just how sensitive these communities are to abiotic conditions; if the microclimates higher on a tree or sapling were different enough than those lower on it to cause community differences there could be a strong case for allogenic succession. Additionally this data would allow a researcher to gain insight into how these

communities may fair in the face of global climate change.

Community Differences Along a Chronosequence

The use of chronosequences made this study cross-sectional rather than longitudinal. This procedure, while highly useful for time-constrained studies like this one, comes with a disclaimer. Of course younger communities found on the tree bark did not necessarily precede the older communities found on the same tree but this technique is commonly used to make inferences about how communities may have changed over time.

PCA score 1 had a significant negative correlation with age at both sites [Fig. 5]. PCA score 1 is a linear representation of multi-dimensional points highlighting their maximal variance. A consistent decrease in this value indicates that the community is shifting away from the species with bi-plot vector arrows pointing towards positive x (component 1 scores) values and towards the species with vector arrows pointing towards the negative x values [Fig. 6]. This means older species are more likely to have *Orthorrhynchium sp.*, filmy fern gametophytes, and *Calypogeia sp.* among others and less likely to have *Leptolejeuna epiphylla*. Unident. lichen A was the most abundant species in the study overall and was usually the first colonizer found on new bark but doesn't account for much variance in the data (its bi-plot vector arrow is largely perpendicular to the PCA score 1 axis) as it is found on lower bark as well. *L. epiphylla* is well known as an initial colonizer because of its rapid growth and loose substrate attach and therefore it is unsurprising that it was present in younger communities but excluded from the later ones where larger bryophytes like *Orthorrhynchium* could outcompete it (Kraichak 2013).

This PCA data when coupled with the significant MANOVA results ($P < .001$) shows that these communities change over time. However there does not appear to be one universal successional trajectory but rather multiple trajectories, even within a single site. These multiple trajectories mean that communities are experiencing divergent rather than convergent succession. Divergent succession isn't "classical" succession by definition but is being increasingly being referred to in recent literature. Leps and Rejmanek (1991) argue that divergent succession can be attributed to the stochastic character of young successional stages and

may represent a facilitative mechanism. In his 2013 study on the epiphytic leaf communities of *Inocarpus Kraichak* was able to demonstrate multiple successional trajectories. He attributed this divergent nature largely to the changing qualities of the leaf surface and microclimate over time. In a similar fashion the bark surface of *Inocarpus* changes extensively over time and although it was beyond the scope of this study a quantitative analysis of this change in microclimate over time deserves further study. Additionally future studies should attempt to look at the biological properties of individual species (such as desiccation tolerance and propagule abundance) to see if these can account for bark age preference and habitat preference.

Investigation into the mechanisms behind this succession were beyond the scope of this study but data like these contribute to a further understanding of the complex community interactions of epiphytes. Additionally this study supports newer theories of divergent succession that are highly dependent on stochastic processes and initial conditions; while the community does shift in a consistent way over time it doesn't converge to a climax community in a way that would support an older understanding of succession.

Interspecific Facilitation/ Inhibition

Unfortunately the DeWitt's replacement series did not yield any results. The bryophytes were not given ample time for growth due to the time constraints of this study and further studies would benefit by allowing 8 weeks of growth instead of 4. Additionally using a coffee grinder or food processor would create a more homogenous bryophyte paint that may facilitate growth. Bryophytes and lichens have been shown to have both facilitative and inhibitory effects on one another and one species may have its range, distribution and proportion within the community largely affected by its biotic interactions with others (Roux et. al 2013).

Species richness was positively correlated with the total amount of epiphyte cover on the bark. Although there was a large variation in cover at each level of species richness when the total cover was averaged for each level and plotted it appeared it appeared to respond logarithmically to increasing species richness [Fig. 8]. This effect could reflect time being necessary for both increased richness and

increased cover but could suggest that there is biotic facilitation and warrant further study.

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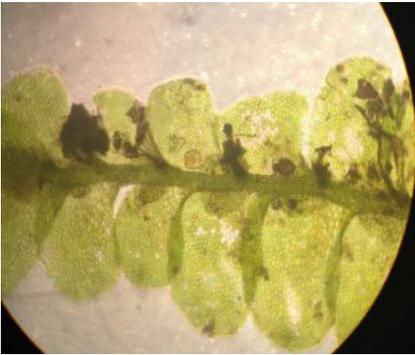
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APPENDIX A

Guide to the epiphytes found on Tahitian Chesnut within Moorea.

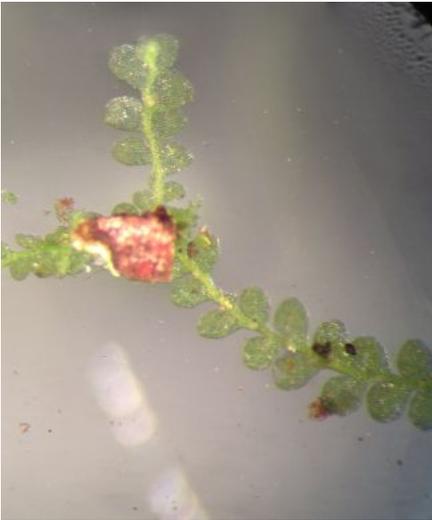
Liverworts



Lophocolea subfusca



Plagiochila sp.



Calypogeia sp.



Leptolejeunea epiphylla

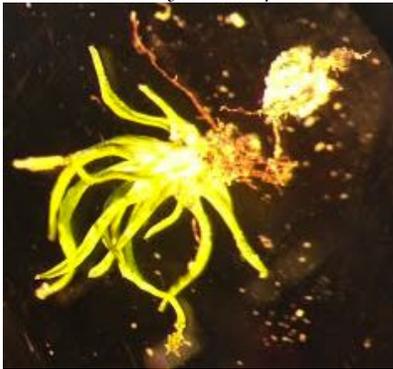
Mosses



Orthorrhynchium sp.



Isopterygium mitten



Calymperes moorei

Lichen



Unidentified lichen A



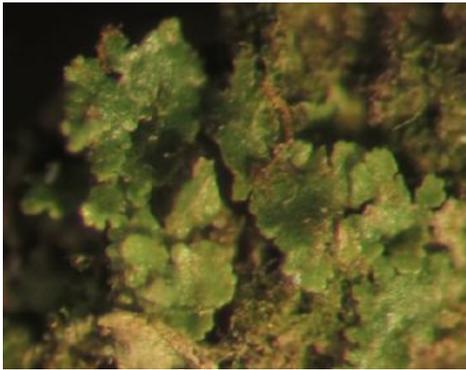
Unidentified Lichen B



Unidentified lichen



Unidentified Lichen D



Caldonia sp.



Unidentified fern

Ferns



Filmy fern gametophyte