

EPIPHYTE COMMUNITY DYNAMICS ON *PEMPHIS ACIDULA* (LYTHRACEAE) ON REEF ISLANDS IN MOOREA, FRENCH POLYNESIA

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Abstract. Tropical forest epiphytes have been shown to be important to net primary production and, in some cases, nitrogen fixation. They have also been shown to be good bioindicators of pollution and are thus important study organisms. This study focused on epiphytes (primarily lichens and mosses) growing on *Pemphis acidula* (J.R. and G. Forster) in Moorea, French Polynesia and the role their environment played in community dynamics. Field sampling and laboratory experiments were carried out on three different motus off of Moorea, focusing on Motu Tiahura where the northeast and northwest sides were sampled, estimating percent cover of epiphytes. Environmental data (aerial cover, lagoon cover, temperature, humidity, wind speed) was recorded from the study sites and relationships between environment and distribution were determined. A total of 9 taxa were found on the motus. Laboratory experiments tested the effect of certain environmental variables on some taxa. The northeast site was much more species rich than the northwest site, though the two environments were not significantly different. Lab results showed significant relationships between light and heat and the moss *Calymperes*, lichen *Physcia cf clementei* (Lynge) and a possible, undetermined lichen. Light, heat and wind most likely limit the abundances of *Calymperes* and *P. clementei* as they contribute to desiccation of the epiphytes.

Key Words: Epiphyte; motu; community structure; *Pemphis acidula*; environmental variation

INTRODUCTION

Tropical zones exhibit some of the highest biodiversity on earth (Scarano 2002), and islands often have unique climatic factors that affect the diversity and abundance of the organisms that live there. Investigating why some species have broader ranges and wider niches than others is a common theme in community ecology (Fridley et al. 2007). The earth provides countless ecological niches and environmental variables, so understanding community dynamics on a small scale is helpful for understanding community interactions on a global scale (Chandy et al. 2006). Niche partitioning becomes more of an

issue when the environment becomes more compartmentalized, because there is more of a gradient of microhabitats in which different species can exist. A classic method of niche partitioning analysis is to observe communities over environmental gradients (Whittaker 1956, Fridley et al. 2007). Several studies (Elston 1995, Wallace 2000, Dobbs 2006) have noted that more community studies of forest epiphytes are needed to better understand their ecology. These studies have all noticed patterns of succession of epiphytes, but little progress has been made to the factors which influence succession. Dobbs (2005) has derived relationships between canopy cover and epiphyte cover as well as species diversity and tree diameter.

An epiphyte is defined as an organism that lives on a plant. Although epiphytes are usually non-parasitic, they will usually gain some sort of benefit from their “host” (Dobbs 2006, Callaway et al. 2002). The general diversity of tropical forest epiphytes is a relatively under-explored territory, especially considering the high percentage of forest biomass and photosynthesis provided by forest epiphytes. Epiphytes also act as good indicators of air quality (Dobbs 2006), so knowledge of their distribution and abundance is important. Lichens, particularly tropical lichens, have also scored very high on anti-cancer screenings (Holl 2002), so it is important to understand more about which environmental factors are favorable for these taxa.

This study focuses on the non-vascular epiphytes, such as lichens and mosses, that live on *Pemphis acidula*, a woody shrub that grows in the unique motu environment in Moorea, French Polynesia. There is little known about tropical epiphytes in general, but the motu environment is perhaps even less well known than main island environments. Motu are small islands that form on top of a barrier reef complex (Murphy 1992). They are formed by the same calcium carbonate-secreting organisms that form coral reefs, such as corals, foraminifera, and coralline algae. As these organisms die, their skeletons remain, forming the reef structure. Motu begin to form when violent storms break up the reef structure and leave a build-up of calcium carbonate rubble (Murphy 1992). They are characterized by this loose rubble substrate as well as a more lithified, calcium carbonate conglomerate platform along their seaward edge (Murphy 1992). The resulting substrate contains large expanses of exposed limestone to be colonized by flora and fauna that prefer drier, windier habitats. *Pemphis acidula* is one of these. On Moorea, it grows only on the limestone substrate characteristic of the motu (Moore 1973). The motu environment is generally quite harsh, with high winds, hot sun, and lot of salt spray.

These factors amplify the threat of desiccation, which greatly affects lichens and mosses, which need moisture to photosynthesize (Benzing 2001). Microclimates also diversify the environment on a spatial scale moving away from the ocean, toward Moorea. Epiphyte diversity would not be expected to flourish here (Yeaton and Gladstone 1982), and yet it does. The unlikelihood of epiphyte success in difficult environments is especially true in the case of mosses, since they generally thrive in low light and high moisture (Benzing 2001).

The objectives of this study are to determine what types of epiphytes live on *P. acidula* on the motu of Moorea, French Polynesia, how the epiphyte communities change on a spatial scale, and how they react to certain environmental stressors. This study also seeks to determine whether environmental stress plays a role in epiphyte distributions and abundances. I postulate that environmental stress does play a role in epiphyte distribution and abundance on the motu, and that epiphyte diversity does change along a spatial scale. To further understand epiphyte distributions, this study tested the tolerances of different epiphytes to different environmental stresses to better get an idea of the degree to which epiphytes are affected by their environments.

MATERIALS AND METHODS

Study site

This study looked at the diversity and abundance of epiphytes on the motu plant *Pemphis acidula*. I chose motu Tiahura (Figure 1b) as my main study site. I also sampled motu Fareone, located just to the west of Tiahura, and motu Ahi, located on the southeast side of Mo’orea near Afareaitu (Figure 1a). I sampled the northeast shores of Tiahura, Fareone, and Ahi to examine the differences in epiphyte assemblages across these motus.

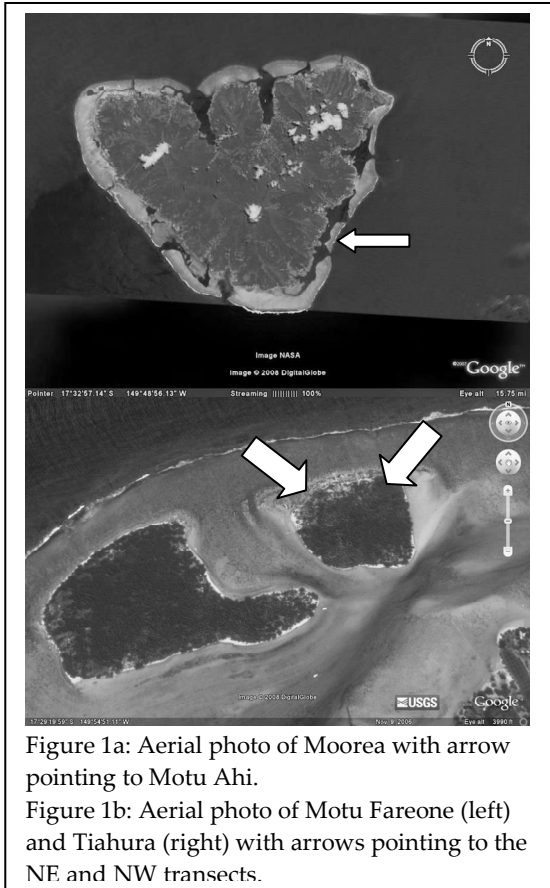


Figure 1a: Aerial photo of Moorea with arrow pointing to Motu Ahi.
 Figure 1b: Aerial photo of Motu Fareone (left) and Tiahura (right) with arrows pointing to the NE and NW transects.

Field sampling

Taxa: In order to understand the distributions of epiphyte taxa on *P. acidula* I sampled the community present in my study site. I sampled along 10 transects 20 m in length on motu Tiahura, sampling the closest shrub to the transect line every 2 m. The transects were split: 5 on the northeast side of the motu and 5 on the northwest. The transects were 3 m apart and ran from north to south. I used a 20 cm x 20 cm grid to estimate the percent cover of epiphytes. Sampling was split up into eight categories. I sampled on the trunk at knee height and breast height and on branches at knee height and breast height. At each of these sites I split the trunks and branches into hemispheres: Exposed (facing the ocean) and protected (facing inland). I used the same protocol in my comparison study between the three motus with some exceptions: the transects were all on the

northeast side of the motus and I sampled every shrub from the conglomerate platform until *P. acidula* was no longer found. I only sampled the exposed hemispheres of the host plants because of difficulty accessing the protected side on motu Fareone. Assessment of the diversity of the northeast and northwest transects were derived by calculating species richness of the two sites and using the Sorenson's index to determine similarity between the two sites. Epiphytes and *P. acidula* sample were deposited at the University of California, Berkeley Herbarium, where they were partially identified.

Environment: I recorded temperature, humidity, wind speed, aerial cover, and lagoon cover at every sampling point. The lagoon cover, which was estimated by holding up a .25 m quadrat at arm's length, was used as a proxy for the amount of salt spray received by the epiphytes. Since the environment on the motu can vary quite a bit, I re-sampled temperature, humidity and wind speed three times and derived averages for the data.

Experimental design

I re-created specific aspects of motu environmental conditions to determine their potential in epiphyte abundance. I chose three representative taxa on which to perform experiments: A possible, undetermined lichen (PUL) found mostly on the exposed, northern part of the sampling area, a grey-green lichen, *Physcia cf clementei* found in the middle of the sampling area, and *Calymperes*, a moss found only in the most protected part of the sampling area. I exposed the samples to various environmental stresses:

a) Light and Heat: experimental samples and control samples of each representative were sprayed with fresh water. The experimental samples were placed in a 45 cm x 60 cm x 50 cm cabinet and a 60 watt bulb was placed 30 cm away. The temperature in the cabinet was 35.5°C and humidity was 31%. The cabinet remained

closed for three days, with observations being made after 1, 2, and 3 days. Within each observation, I measured taxon-specific indicators of stress: PUL percent bark coverage, soredia production, and color quality; *P. clementei* percent bark coverage, apothecia production, color quality; *Calymperes* percent open leaves, percent brown leaves, color quality. I repeated the whole trial twice for a total of three trials.

b) Wind: experimental samples and control samples of each representative were sprayed with fresh water. The experimental samples were placed in a cabinet and a small fan was placed 45 cm away from them. The fan moved from side to side, varying the wind speed in the chamber from .5 m/s to 2.5 m/s. The cabinet remained closed for three days, with observations being made after 1, 2, and 3 days. Within each observation, I measured the same response variables used in the light and heat trials. I repeated the whole wind trial twice for a total of three trials.

c) Salt Water and Fresh Water: I took six samples of each genus plus a control sample and divided them up into high, medium, and low designations. Three samples received daily sprays of fresh water while the other three samples received daily sprays of salt water. Low samples received 5 sprays, medium received 10, and high received 15. These samples were placed in a cabinet along with a control group, which received no treatment. Over a period of two weeks, daily observations of all samples including the control were made as to the percent of bark covered by epiphytes, percent of water covering epiphytes, amount of water pooling in the Petri dish, and other genera-specific indicators of stress.

Statistical analyses

Epiphyte and environmental sampling data: I used linear regression analysis to test the significance of abundance of each epiphyte taxon as compared to the distance from the

ocean to the north and the lagoon from the east and west. I also used linear regression analysis to see how the environmental data varied with distance from the water. I compared the 5 northeast transects to the 5 northwest transects both in terms of epiphyte cover, and environmental variables, using T-tests.

Experimental data: To test the significance of my lab results, I used a T-test to see how the treatment effects differed from each other and from their controls. I tested the significance of similarity between epiphyte sampling data of the taxa used in the lab experiments and environmental sampling data using a linear regression analysis. All statistical analyses were performed using JMP 7®.

RESULTS

Field sampling

Taxa: Nine epiphyte taxa were found on the northeast side of motu Tiahura, while six taxa were found on the northwest side of the island (Table1). The Sorenson index showed that the

Taxa in Northeast Site	Taxa in Northwest Site
Possible, undetermined lichen (PUL)	PUL
<i>cytonema</i> with fungus	<i>Scytonema</i> with fungus
Graphidaceae lichen	Graphidaceae lichen
<i>Chrysothrix cf candelaria</i>	<i>Chrysothrix cf candelaria</i>
<i>Physcia cf clementei</i>	<i>Physcia cf clementei</i>
<i>Collema cf conglomeratum</i>	
GrCL (Green, crustose lichen)	
<i>Calymperes</i>	
Liverwort	

Table 1: List of taxa found in the NE transects (column 1) and NW transects (column 2)

two sites were 71% similar ($\beta=.7058$). Two of those taxa were the most abundant in both sites: PUL (average percent cover=26.38 northeast and 27.64 northwest) and a black crustose lichen, *Scytonema* with fungus (average percent cover 3.9175 northeast and 5.7663 northwest). The northeast side also

Taxon	F-value	DF
<i>Calymperes</i>	.0003	1
<i>P. Clementei</i>	.0276	1
<i>Scytonema</i> with fungus	.0007	1
Graphidaceae	.0024	1

Table 2: Taxa with a significant relationship with distance from the ocean

saw two more taxa with relatively high abundances, though they were not found in high abundances on the northwest side: *Physcia cf clementei* (average percent cover=3.10 northeast and .002 northwest) and the moss genus *Calymperes* (average percent cover 2.50 northeast and 0.38 northwest). *P. clementei* and the moss *Calymperes* were only found in any abundance in the northeast transects, however general observation of *Pemphis* epiphytes farther into the forest in the area of transects the northwest transects showed a higher abundance of these taxa.

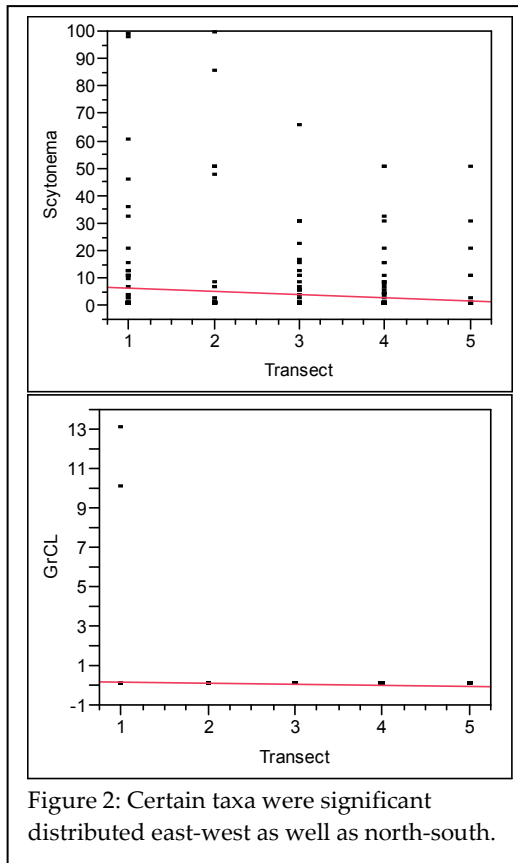


Figure 2: Certain taxa were significant distributed east-west as well as north-south.

There was a definite trend in epiphyte distribution. In the NE transects, the presence of *Calymperes* and three lichens (*P. clementei*, *Scytonema* with fungus, and a lichen in Graphidaceae) were significantly related to distance from shore according to linear regression results (F=.0003, .0276, .0007, .0024, respectively) (Table 2). GrCL (F=.0469, DF=1) and *Scytonema* with fungus (F=.0188 DF=1) were significantly distributed by transect, meaning running from east to west (Figure 2). There were no significant distributions by meter or by transect in the northwest transects. Generally only lichens were found in the most exposed areas of the motu, near the conglomerate platform, meters 2-6. PUL (possible, undetermined lichen) and *Chrysothrix cf candelaria* (J.R. Laundon) were in highest abundance in the northeast site, with average covers of 22.70% and 4.45%, respectively (Table 3). PUL also dominated in the seaward portion northwest site (average percent cover 25.82), but the next most dominant was *Scytonema* with fungus with an average cover of 3.50% (Table 3). The same

Transect	Meter	PUL average % cover	<i>C. candelaria</i> average % cover	<i>Scytonema</i> average % cover	<i>P. clementei</i> average % cover
1-5	2-6	22.70	4.45	X	X
1-5	16-20	27.52	X	X	4.68
6-10	2-6	25.82	X	3.50	X
6-10	16-20	30.41	X	6.08	X

Table 3: Epiphyte dominance by distance from the shore. PUL remained dominant but the next dominant species changed as distance got greater.

northwest species dominated in the inland portions of the transect (meters 16-20), with average cover being 30.41 and 6.08, respectively (Table 3). Dominance changed in the inland meters in the northeast transects, with *P. clementei* replacing *C. candelaria* as the second most dominant species (average cover=4.68%). PUL remained the most dominant inland (average cover=27.52%) (Table 3). Epiphyte dominance was similar across motus. (Table 4). PUL was the dominant species and *Scytonema* with fungus

was the second most dominant species in all threemotus.

Motu	Species Richness	PUL average % cover	<i>Scytonema</i> average % Cover
Fareone	2	38.47	26.81
Tiahura	6	34.42	32.10
Ahi	3	50.71	26.43

Table 4: Epiphvte dominance across motus.

Environment:

The most striking aspect of the motu environment is how changeable it is. The temperature seemed to be the most constant, remaining around 35°C most of the time. Humidity was quite variable, ranging from 40% to 70% depending on the day. Wind speed (Figure 3) was perhaps the most varied during the study, between days as well as between sites. Motu Ahi had the windiest days, with speeds often over 10 m/s. Motu Tiahura was less windy, especially in the northeast transects. Wind speeds ranged from 0 m/s to 8 m/s depending on the location within the sample site or the day. Aerial cover was consistently high, at least 90%, except at Motu Ahi, where the average aerial cover was

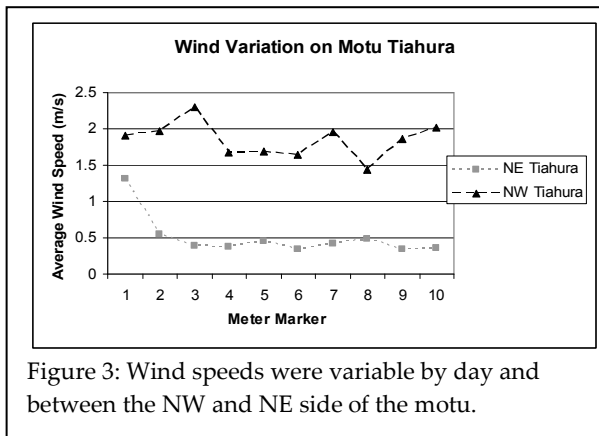


Figure 3: Wind speeds were variable by day and between the NW and NE side of the motu.

around 50%. Lagoon cover varied a little more than aerial cover. The two short transect sites had differently shaped conglomerate platforms, which changed the amount of exposure they would get from the ocean. The northeast were more exposed, with coverage

ranging from 45% to 95%. The northwest were better covered, with coverage ranging from 90% to 99%. Temperature, lagoon cover and wind speed were significantly related to distance from the shore in the northeast transects, with F values being .0262, .0001, and .001 respectively (DF=1 for all three). In the northwest, aerial cover (F=.0102, DF=1) and lagoon cover (F=.0001, DF=1) were the only environmental factors to be significantly related to the meter mark. Between the northeast and northwest transects, the only taxon that was distributed significantly differently but still present in both sets of transects was *Collema cf conglomeratum*

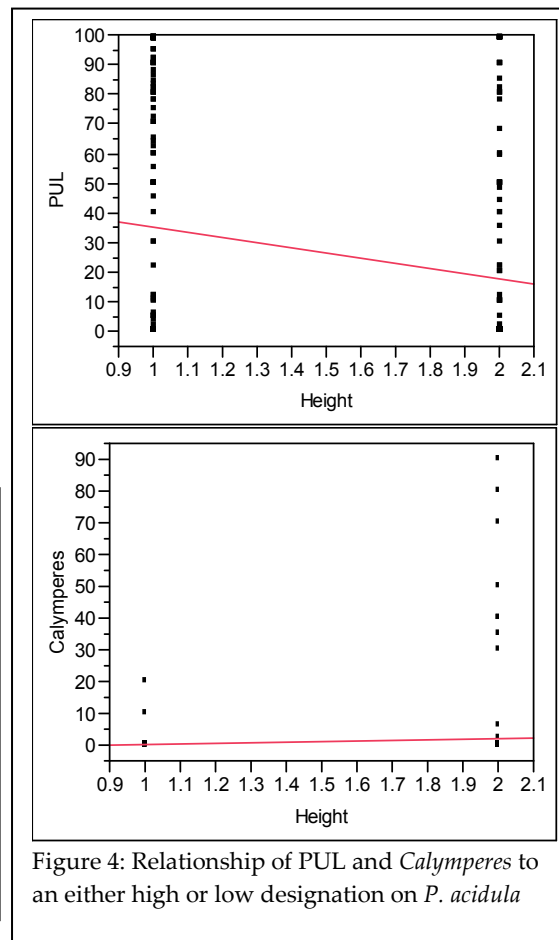


Figure 4: Relationship of PUL and *Calymperes* to an either high or low designation on *P. acidula*

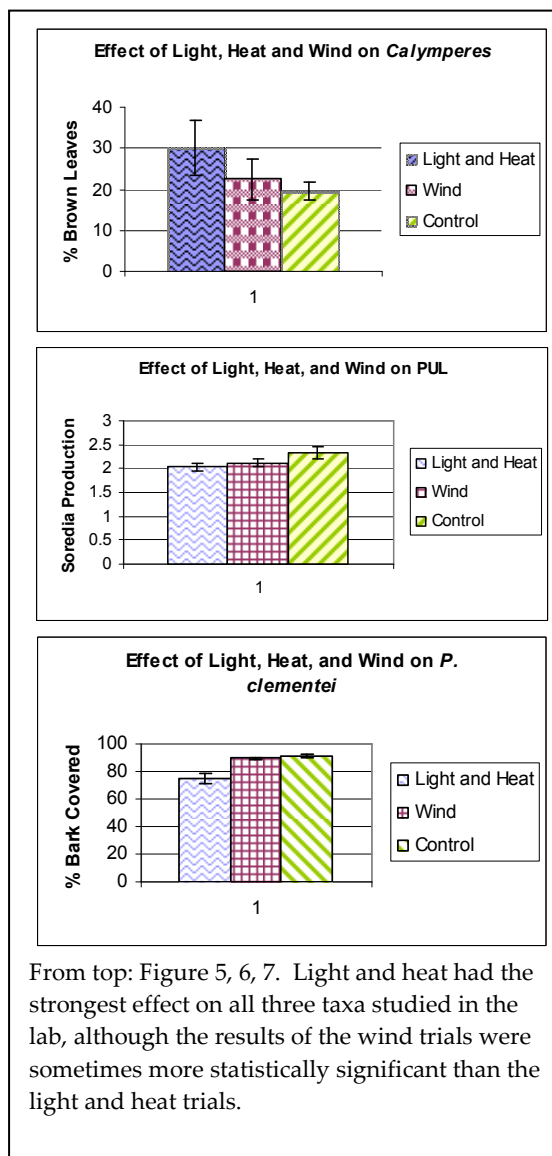
(Hoffm.) (p=.0022).

There were no significant differences between the environmental data in the northwest and northeast transects. There was no significant relationship between exposure

and taxa in the northeast or northwest transects. In the northeast transects, *Calymperes* was significantly related to height, being more abundant at higher points of the shrubs ($F=.0122$ $DF=1$) (Figure 4). A lichen in Graphidaceae ($F=.040$ $DF=1$) and PUL ($F=.0001$ $DF=1$) were significantly more abundant at lower designations (Figure 4). PUL was the only species with a significant relationship to height in the northwest transects, again being clustered on the lower regions of *P. acidula* shrubs ($F=.0001$ $DF=1$). Environmental factors did not change significantly across motus.

Experimental results

a) Light and Heat: PUL was most affected by heat. The PUL samples started to turn brown after the first day in each experimental



trial. The heat trials also showed *Calymperes* leaves to be shriveled and became 10-25% more brown after the first day. By the fourth day in all trials, *Calymperes* samples were mostly brown and likely dead. *P. clementei* became a little bit lighter in color, but spore production remained pretty much constant throughout the trials.

b) Wind: Wind also showed some differences in the epiphyte appearances compared to the control. The lichens were a little paler in color, possibly dried out, and PUL started to turn brown by the end of each trial. *P. clementei* showed a difference in spore count and *Calymperes* showed a difference in leaf opening and color.

The results of the wind T-test showed that wind had a significant effect on the percent bark coverage ($p=.048$), soredia quality ($p=.048$) (Figure 5), and color quality ($p=.0006$) for PUL compared to the control. Light and heat as well as wind T-test results showed significant limitation in percent bark coverage and production of apothecia in *P. clementei* (Table 5, Figure 6). Wind was shown to significantly contribute to the browning of *Calymperes* leaves, with $p=.049$ (Figure 7).

c) Salt Water and Fresh Water: There were many similarities in the results of the salt water and fresh water experiments. However, based on one observation, the salt water had more of an effect on the epiphytes than the fresh water in most cases. The salt water treatment caused *P. clementei* spores to grow in higher numbers than the control. The medium designation saw an increase for 20 to 27 spores while the high designation saw a loss of 9 to 0. *Calymperes* samples were brownish black by the end of the salt water trial, with the "high" setting being the brownest (Figure 8). The brown coloration likely shows that the moss did not survive the salt spray. The salt water also seemed to keep the bark more intact when water started to pool in PUL Medium and High, and more of the actual lichen flaked off of the bark.

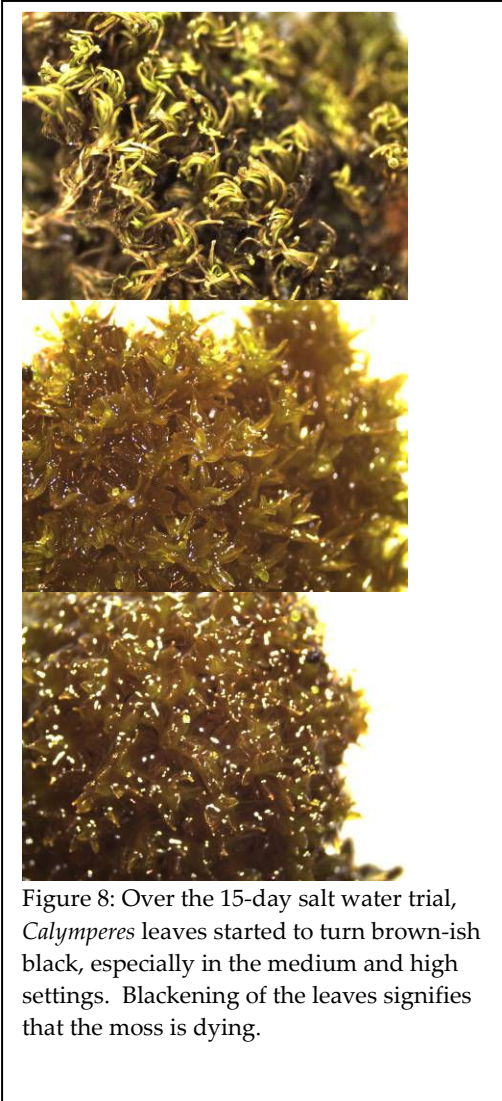


Figure 8: Over the 15-day salt water trial, *Calymperes* leaves started to turn brown-ish black, especially in the medium and high settings. Blackening of the leaves signifies that the moss is dying.

In general, the early stages of the water experiment benefited the epiphytes. They all did well up to a point, and then the excess water seemed to be harming them. *P. clemenei* and *Calymperes* seemed to thrive the most from fresh water at the beginning of the trial, based on one observation. Even after the first day, it seemed like PUL was overwhelmed by the amount of water distributed in the “high” sample. By the fourth day, water was pooling in the PUL High plate and the lichen was flaking off. The same thing happened to *P. clemenei* by the 11th day. *Calymperes* was harmed by excess water by the 12th day, when the low, medium, and high samples were all completely covered with water and the high

samples had turned black/brown, signaling that the moss had died.

Of the taxa used in the lab trials, only *P. clemenei* and PUL had a significant relationship with environmental data in the field. *P. clemenei* was significantly related to aerial cover ($F=.0517$ $DF=1$) and lagoon cover ($F=.0002$ $DF=1$) (Figure 9).

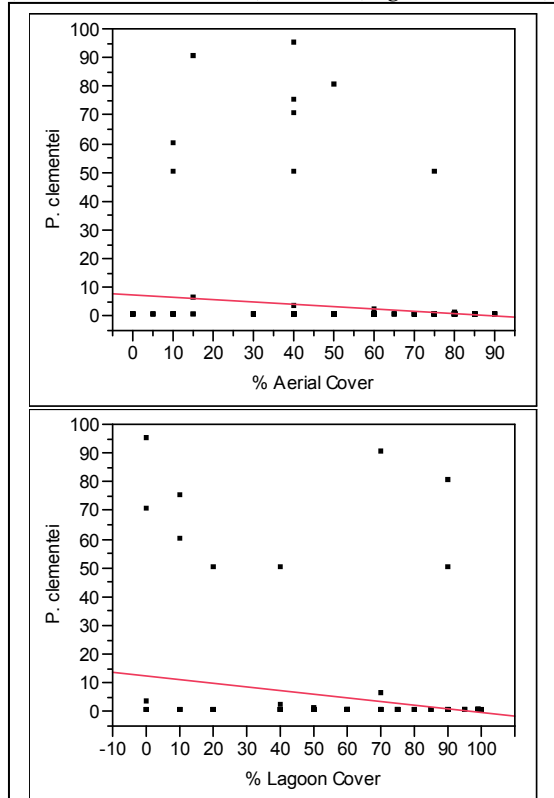


Figure 9: The relationships of *P. clemenei* with lagoon cover and aerial cover. The lichen has an inverse relationship with both.

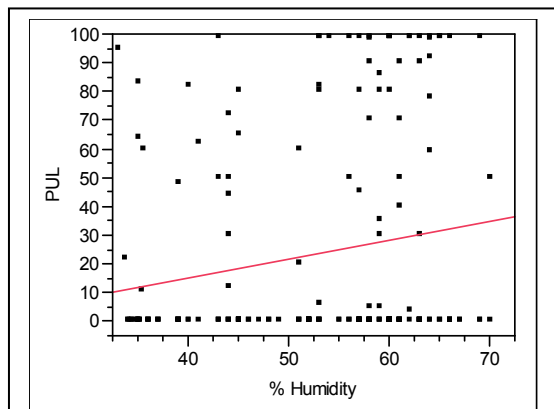


Figure 10: The relationship of PUL and Humidity

PUL was significantly related to humidity ($F=0.0113$ $DF=1$) (Figure 10) in the northeast transects and aerial cover ($F=0.0136$ $DF=1$) in the northwest transects. The distribution of *Calymperes* was not significantly related to any environmental variable.

DISCUSSION

Epiphyte distribution and abundance

Within the northeast and northwest transects on Motu Tiahura there was only one species, PUL, that was significantly more dominant over the others, with an average cover of around 27%. In all cases, the next-most dominant species had an average cover of 5% or lower. The over-representation of PUL could be attributed to its high tolerances for environmental stressors pending identification.

Identification of the epiphytes showed that the most dominant epiphyte in the study, a possible, undetermined lichen (PUL) may not be an epiphyte at all. It was reported as possibly being arthropod activity on the *P. acidula* bark. There are many implications for the limitation of epiphyte growth if this is the case. First, epiphyte abundance is much lower than was once thought. As stated earlier, PUL was by far the most abundant epiphyte found in the entire study, far surpassing others in terms of average percent cover. If PUL turns out to be arthropod activity, the second most abundant epiphyte becomes the most abundant, and overall epiphyte abundance is reduced by at least 30%. This could mean that the factors that limit the success of epiphytes on *P. acidula* have a much more drastic effect than what was previously observed. Also, the high occurrence of arthropod activity could imply that predation may be a limiting factor for epiphytes on *P. acidula*. Turner (1984) states that arthropod predation pressure is a factor in epiphyte growth in the temperate zone, and this idea could easily be transferred to the tropics.

The distribution of *P. acidula* may provide some insight into the low abundance of epiphytes in the NW transects. The substrate for *P. acidula* varied greatly between the northeast transects and the northwest transects. The main substrate on the northeast side of the motu was sandy beach formed from erosion of coral rubble. The main substrate on the northwest side of the motu was the hard, calcium carbonate conglomerate platform, which is mainly comprised of fossilized coral. Although a conglomerate platform did exist on the northeast side, *Pemphis* did not grow very successfully there. It grew in greater stands on the northwest conglomerate platform as well as the sandy beach that lay behind it, although this area lay outside of the transect zone. Interestingly, when the epiphyte diversity on these inland shrubs was examined, taxa were found that were similar to the inland patches on the northeast side, such as *Calymperes* and higher levels of *P. clementei*. The presence of more *P. acidula* on the conglomerate platform may mean that the northwest side of the motu is more conducive to plant growth in general, but it is interesting that epiphyte diversity remained somewhat low until it reached the inland patches. Perhaps the *Pemphis* that grows on the sandy substrate can more readily host epiphyte taxa, which is why diversity was so much higher on shrubs on the sandy beach.

Experimental outcomes versus distributions

Calymperes was the only moss found in this study, and it was found in relatively high abundances in some areas, namely the inland patch of the northeast transect. Although the moss did not seem to be in its healthiest state on the motu, and the freshwater test showed that the moss thrived with a somewhat higher moisture exposure, and it may be that this moss can outcompete other lichens in conditions of higher water availability. The inverse relationship of *Calymperes* and wind supports this idea, since less wind means less

desiccation and therefore more moisture. *Calymperes* was also limited to the inland shrubs, most likely because of the lack of salt spray in the inland area, as seen through the relationship of lagoon cover with depth. Lagoon cover was the highest inland, meaning less salty air would reach the inland epiphytes, and *Calymperes* was most negatively affected by salt water in the laboratory observation.

The lack of a difference in epiphyte distributions on the exposed versus the protected side of *P. acidula* is most likely explained by the lack of aerial cover that the *Pemphis* stand has on the motu, especially among the southwest transects. In much of the study area, *Pemphis* is either the only plant present or is the tallest plant, meaning it receives direct sunlight much of the time. Because of this, desiccation-causing factors such as light and heat will still affect epiphytes on the protected side of the shrubs. However, this open situation does not explain the role of wind or salt spray on *Pemphis* epiphytes. The high winds present on the motu, particularly on the outermost strand of plants facing the ocean, are thought to be a limiting factor for the distribution of some of the epiphytes, particularly as a carrier of salt spray. Secondary observations of the distribution of *P. acidula* may give clues as to why the distribution of epiphytes were not related to wind speed patterns and lagoon cover in a significant way. Often, there would be lagoon exposure from more directions than what was recorded, particularly on the eastern-most and western-most edges of the study sites. It is entirely possible that this extra exposure limited epiphyte abundance, and it may have been a good idea to account for the extra exposure during sampling.

Spore production in the *P. clementei* salt water test shows that the lichen was more reproduce, based on the occurrence of apothecia (spores), under a medium amount of salt spray. The question remains as to whether the occurrence of apothecia is a sign of health, whether lichens reproduce in

favorable conditions, or a sign of the last throes of survival, reproducing as a last resort. It would seem that production of apothecia is quite energy-intensive, and given the slow growth of lichens (Ellis and Coppins 2007), it would make sense that they would not produce spores until it is absolutely necessary. In fact, Honegger (1996) states that foliose lichen *Xanthoria parietina* (which is morphologically similar to *P. clementei*, though is a different color) will produce apothecia more readily along "drought-stress induced cracks". Even though the medium and high levels of salt water had proportionally the same amount of salt, either the extra salt the extra water that came with the higher amount of sprays stopped the production of apothecia. The response of the experimental taxa to the fresh water test tended to show, after one observation, a saturating curve of positive response to fresh water. This result shows that perhaps the taxa found on the motu are adapted to use water efficiently and can become overwhelmed by excessive amounts of fresh water. Lichens and mosses exhibit poikilohydry, a condition where plants readily equilibrate their water content to the environment, usually conjoined with mechanisms of desiccation-tolerance (Mishler 2003). Taking poikilohydry into account, it is not surprising that lichens and *Calymperes* dominated the diversity of epiphytes on the motu.

The significant effect that light, heat, and wind had on *P. clementei* indicates that these factors may limit the growth of the lichen. This makes sense, as lichens have been historically shown to be limited by sunlight exposure (Hilmo 2002). The positive relationship between aerial cover and *P. clementei* supports this idea.

However, it may be that a windy environment can actually be helpful to some lichens that use wind as a dispersal mechanism. Some lichens disperse by wind after fragments break off from the main thallus (Campbell and Reece 2004). It may be that the lichens found on the outer edges of

the transects, where wind speeds were the highest, disperse this way.

In order to fully assess the role of environmental variables on the dynamics of this epiphyte community, it is necessary to carry out more laboratory experiments, perhaps on different taxa, to narrow down the environmental variables and the degree to which they affect the epiphytes. Identification of the epiphytes is also extremely necessary as taxa-specific research will provide much insight into the theoretical tolerances of the epiphytes observed. More epiphyte community studies would also shed light on the overall interactions of tropical epiphytes. The motu environment, unique and albeit temporary, provides a model of an island within and island that demonstrates the intricacies of ecological interactions. The diversity and abundance of epiphytes on *P. acidula* is merely one example of community dynamics within a vast expanse of Earth's biodiversity.

Conclusions

Consistent with the hypothesis, epiphyte diversity does change on a spatial scale and to some extent varies with the environment. While the most dominant taxa, PUL was the most dominant taxa throughout the study, though identification of the epiphyte remains unclear. What was thought to be a lichen may turn out to be arthropod activity, which would change the implications of the study. Regardless, PUL did change on a spatial scale. The second most abundant taxa were different in areas closer to the ocean and more inland. Specifically, *P. clementei* replaced *C. candelaria* on the northeast transects in the more inland patches. The environment did not seem to vary across motus, nor on different sides of the same motu, though it was variable from day to day. Wind speed was particularly variable from day to day. Some taxa showed significant responses to the environment in the field, and laboratory observations showed signs of a hypothetical response to the same

variables, most noticeably in *Calymperes* and its reaction to salt water.

Light, heat, and wind also had significant relationships to response variables of PUL, *Calymperes*, and *P. clementei*. These environmental variables are most likely limiting factors for *Calymperes* and *P. clementei*, but more experimental procedures are needed to determine whether salt water and fresh water are factors that significantly affect the distribution and abundance of epiphyte on *P. acidula*. It would be interesting to investigate the epiphyte-host relationship further to see if the success of *P. acidula* is in fact a limiting factor for its epiphytes.

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