THE COMPOSITION OF BRYOPHYTE COMMUNITIES ON LIMESTONE VERSUS BASALT SUBSTRATES IN COASTAL AND MID-ELEVATION FORESTS OF MO'OREA, FRENCH POLYNESIA

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Abstract. Communities of non- vascular plants called bryophytes grow on limestone and basalt on Mo'orea, French Polynesia. The abiotic properties associated with living on each substrate is not well known, however. This study looks at the soil pH, buffering capacity, phosphate levels and substrate water holding ability associated with each substrate. In general, limestone has greater water holding capacity than basalt and its soils are more basic, have higher phosphate levels and have a greater pH buffering capacity than soils on basalt. This study also looks at the biological impact of these substrate abiotic differences by using multivariate discriminate analysis to compare bryophyte communities on each substrate. Five species are tightly correlated with a particular substrate. *Ectropothecium sandwichense* and *Floribundaria aerunginosa* prefer limestone whereas *Calymperes aongstroemii*, *Taxithelium vernieri*, and *Ectropothecium sodale*, prefer basalt. Because the distribution of these species is highly correlated with substrate in nature, a reciprocal transplant experiment was designed to see if substrate directly affected a specie's growth. *Ectropothecium sodale* and *Ectropothecium sandwichense* can, physiologically, grow on either substrate. This suggests that other factors like elevation, predation and community effects might be contributing to the segregated bryophyte communities observed in nature. Understanding the abiotic and potential biotic factors that influence the distributions of bryophytes enables locals, scientists and developers to use these plants as bioindicators of habitat change.

Key words: Mo'orea, French Polynesia; plants; bryophyte; bioindicators; abiotic; substrate; limestone; basalt; soil pH; buffering capacity; phosphate; water; distribution; Ectropothecium sandwichense; Floribundaria aerunginosa; Calymperes aongstroemii; Taxithelium vernieri; Ectropothecium sodale

INTRODUCTION

Understanding the distributions of plants offers insight into their geographic ranges and ecology and enables managers and conservationists to determine which habitats are most important to particular plants of interest. In addition, scientists and environmentalists may use the presence or absence of certain plant species as bioindicators of abiotic conditions in an area. There are many abiotic factors that affect the distributions of plants. Two important factors are water availability and the relationship between substrate pH and nutrient availability. Water is important for all plants, in part as a medium for transporting nutrients like nitrates and phosphates, and is also important for reproduction purposes in plants like bryophytes and ferns (Raven 2011). Substrate pH is important to plants because pH affects the amount of bioavailable micro- and macronutrients, like phosphorous, (Bailey 1996) which is important for DNA synthesis. One group of plants that is particularly sensitive to these factors is bryophytes- a group that includes: mosses, liverworts and hornworts.

Compared to other plants, this group is especially sensitive to atmospheric and substrate conditions because of its unique structural and physiological adaptations. For example, because they lack a vascular system, true stems and roots, bryophytes are low growing plants that instead rely on structures called rhizoids to anchor them close to substrate surfaces and thin leaves to absorb water and mineral nutrients through osmosis (Stotler & Crandall-Stotler 2010). In mosses and liverworts, these leaves lack a protective epidermis and cuticle making them highly sensitive to nutrient, pollution, pH and water variations (Saxena 2004). Bryophytes can also regenerate from protonema (Giles 1971) but only under suitable conditions. The low growing nature, modified leaves and regenerative ability of bryophytes make them highly sensitive to substrate abiotic conditions and potentially excellent bioindicators of substrate conditions. Despite sharing key morphological structures, however, bryophytes include a very diverse group of plants that respond differently to different abiotic conditions. For example, of the 28,000 species of known bryophytes worldwide (Sabovljevic 2008), many are physiologically distinctive, with specific water (Vincke et al. 2004) and substrate preferences (Gignac 2001). In terms of moisture preference some species like *Breutelia integrifolia* (Taylor) A. Jaeger, typically found on the edge of lakes and rivers, prefer very wet environments while others like *Selaginella uncinata* (Desv. ex Poir.)Spring, typically found in Antarctica, prefer less humid environments, (Vincke *et al*. 2004). In terms of substrate preference there are two commonly recognized groups of bryophytes called calciphiles (calcium loving) and acidophiles (acid loving) (Mueller 2000). For example in the Appalachian Mountains, *Polytrichum* sp. and *Dicranum* sp. are confined to more acidic habitats whereas *Atrichum* sp. is denser in alkaline habitats (Mueller 2000). Since bryophyte distribution appears to be, at least, partially influenced by moisture level and substrate conditions in other parts of the world, it would be interesting to see if these trends are prevalent in the low and mid elevation forests of Mo'orea.

Mo'orea is a high volcanic island. Due to its volcanic origins, Mo'orea is dominated by silica rich basalt formed from rapidly cooled lava (Bas *et al.* 1986). However, Mo'orea also has coral-derived limestone, composed mostly of calcium carbonate (Bliss *et al*. 2008), in both coastal (8.8- 10.9 meters above sea level) and mid-elevation (152.4-207.2 meters above sea level) forests. In coastal forests, the limestone may be present as a result of hurricanes tossing coral boulders ashore from the lagoon (Wells et al. 2010). In higher elevation forests, however, limestone can only be present via human activities. On Mo'orea, limestone can be found on archeological sites called *Marae*. *Marae*s are walled religious temples with a raised *ahu* (altar) built by Eastern Polynesians before European contact (Kirch 2000). The walls and steps of *marae*s were constructed from basalt whereas the *ahu*s and their platforms were often faced with live corals from the lagoon (Sharp et al. 2010). Although many of these *marae*s have been torn down and abandoned since the 1700s (Sharp et al. 2010), their coral and basalt ruins still remain today with communities of bryophytes living on them. This provides a natural experiment for assessing bryophyte communities on two very different rock types at higher elevations: one common and natural (basalt), the other rare and introduced by humans (limestone).

This study examined the composition of bryophyte communities on two different substrates, basalt and limestone, at low and mid elevation rainforest habitats and surveyed the microhabitats that the bryophytes were growing on. The goals were to determine whether there is an association between particular species of bryophytes with a particular substrate and to consider possible abiotic differences between the substrates as possible explanations for this distribution. The abiotic factors that were studied are substrate water retention, soil pH, buffering capacity, and phosphate levels. To answer the question of whether a bryophyte species is associated with a substrate, a quantitative field survey of the species compositions of bryophytes on limestone and basalt was done at both low and mid elevation forest sites. In addition, a reciprocal transplant study, taking advantage of a bryophyte's ability to regenerate from protonema (Giles 1971), was done to see if the substrate differences directly affected bryophyte growth. Due to the chemical and physical differences between the substrates and the existence of calciphilic and acidophilic bryophytes with different abiotic preferences around the world, I hypothesized that: (1) the abiotic factors, associated with living on each substrate, will be different; (2) the bryophyte species composition will be completely different between the two substrates and between low and mid elevation forest sites; and (3) the dominant basalt bryophyte will not grow in culture on limestone and vice versa.

METHODS

Bryophyte collection and identification

I surveyed coastal and mid-elevation forest sites on Mo'orea, French Polynesia from 9/24/2012- 11/14/2012 for bryophytes growing on limestone and basalt [Fig. 1]. The collection sites included: 1. a *marae* site before reaching a banyon tree next to the "Three Pines" trail (17˚31'58.26"S, 149˚49'46.50"W). 2. a *marae* site just pass the banyon tree on the same trail (17˚32'8.46"S, 149˚49'31.68"W). 3. a *marae* site further away from the banyon tree also on the same trail (17˚32'8.28"S, 149˚49'31.26"W). 4. a coastal forest in the mangrove ferns near Oponahu Bay (17˚31'1.26"S, 149˚50'59.28"W). 5. a coastal forest on the Kellum property (17˚30'46.50"S, 149˚50'58.14"W). 6. a coastal forest in between the mangrove ferns and Kellum property next to a stream (17˚30'59.76"S, 149˚50'57.96"W). I collected all bryophytes on rocks that looked different by either using my fingers to gently peel them off or using a chisel to scrape them off. The bryophytes were placed in centrifuge tubes until brought back to the Gump Station for identification using Leica dissecting and compound microscopes and the Whittier (1976) key. Once identified, the bryophyte was taped to a piece of paper to create a reference key for use in the field composition survey. Voucher specimens were also collected and shipped back to UC Berkeley in paper envelopes and identified with help from the Mishler lab.

Field composition survey

At each site, I tossed a pencil in the air and walked towards the direction that the eraser

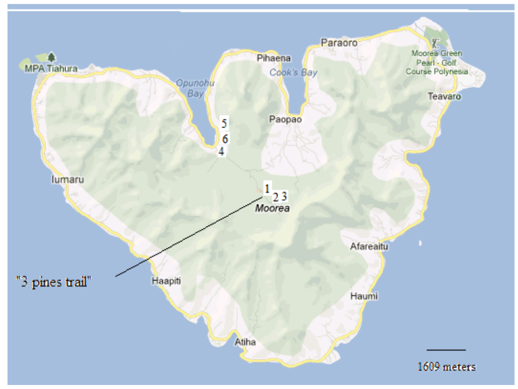

FIG. 1. A MAP OF STUDY SITES (GOOGLE MAPS 2012). SITES "1", "2", "3" ARE MID-ELEVATION SITES AND "4", "5" ,"6" ARE COASTAL SITES.

pointed until I came across a pair of rocks. 7 rock pairs of basalt and limestone were surveyed randomly using this method. Rocks were considered a pair if they were within one meter of each other. Next, I identified the bryophytes living on each rock and placed a .29 meter by .29 meter quadrant with 1,936 squares over each rock and counted the number of squares that the rock took up. This gave me the surface area of the rock. To get percent area composition for each bryophyte, I counted the number of squares that a bryophyte filled, recorded this, and divided it by the number of squares that the surface area of the rock occupied. A multivariate discriminate test was done between all species for the two substrates to assess how similar the communities were between substrates. The same test was done for all species for the two elevations to see how similar the communities were between coastal and mid elevations. For each species, 1-way ANOVAs looking at elevation and substrate effects separately were done to see if these parameters were important for influencing their distributions.

Abiotic conditions: soil collection and tests

After the composition survey was done, I removed the bryophytes off the substrate with a chisel and shook them to release the soil under them. This soil was combined with the soil on top of the, now bryophyte barren substrate, and scooped into a container. The limestone and basalt soils were kept in separate containers, brought back to the Gump station and dried in an oven overnight. Dry soils were used for testing. Seven soil pH and buffering capacity tests, and three phosphate tests (due to a shortage of phosphate indicator) were run for soils on basalt at each site using a Lamotte soil testing kit (code 35880; LaMotte, Chestertown, MD, USA) to measure pH and phosphate levels. Gas volume was measured by reacting 1.5g of soil with an excess of 24% hydrochloric acid in a centrifuge tube and funneling the gas evolved into an inverted graduated cylinder filled with water [Fig.2]. The amount of water displaced by the gas was measured as an estimate of soil buffering capacity with greater gas production representing greater soil pH buffering capacity. The same tests were done for soils on limestone. Soil phosphate level, pH and buffering capacity were each averaged across elevations and analyzed using one-way ANOVAs between substrates.

Abiotic conditions: substrate water holding capacity and retention

36 rocks, 18 basalts and 18 limestones, were collected from the Gump station and boiled in water for 30 minutes and scrubbed with a toothbrush to kill and remove anything living on them. The rocks were dried overnight and the dry weight of each rock was recorded. The rocks were then submerged in water for 15 minutes and reweighed to get wet weight. The maximum substrate water holding capacity was calculated with wet weight minus dry weight. The wet rocks were reweighed after 60 minutes in an oven to determine rate of water loss. 24 of the rocks were then fully dried for use in the growth experiment. Substrate water holding capacity and retention was averaged across elevations and analyzed using one-way ANOVAs between substrates.

Growth manipulation: effects of substrate

Two bryophytes, *Ectropothecium sandwichense* (Hooker and Arnott) and *Ectropothecium sodale* (Sull) Mitt, found to be

FIG. 2. APPARATUS USED TO MEASURE A VOLUME OF GAS FROM SOIL AND ACID REACTION

dominant on limestone and basalt, respectively were collected. 2.3 grams of the basalt dominant species was blended with 100mL of water to make the basalt dominant paint (BDP). The same was done for the limestone dominant species to make the limestone dominant paint (LDP). The blending was necessary to create protonema which can regenerate into a new bryophyte. BDP was painted onto 6 basalt rocks as a control. BDP was painted onto 6 limestone rocks to see if it would grow. The same was done for LDP on 6 other basalt and 6 limestone rocks. The 24 rocks were placed in two slightly open plastic containers near a window away from direct sunlight. Inside the containers, the rocks were placed on elevated petri dishes with holes, for drainage, and surrounded by a pool of water outside the dishes to maintain humidity. The rocks were sprayed daily using tap water and pictures of each rock with the bryophyte on it were taken at the start of the experiment and after 4 weeks to assess growth by measuring plant length using ImageJ (Abràmoff 2004) software. One-way ANOVA's were done to see if a species grew at a different rate on different substrates.

RESULTS

Abiotic conditions: substrate water holding capacity and retention

TABLE 1. Summary of average abiotic conditions associated with basalt and limestone.

Substrate	pH	Buffering capacity (mL of gas)	Phosphate Level (lb Acres/ 6"soil)	Water Cap. (g water/ g rock)	Water Ret. (% of max after 1 hr)
Basalt	↓= 6.9	↓= 10.3	↓= 16	↓=0.008	↓= 41
Limestone	↑= 7.8	↑= 1.3	↑= 10	↑= 0.1	↑= 88

Note: All properties differences are statistically different $P < 0.005$

A gram of limestone holds significantly (P= 0.0001) more water than a gram of basalt by 0.0992 grams of water. On average a gram of limestone can hold 0.1 grams of water whereas a gram of basalt can hold 0.008 grams. Limestone retains significantly (P=0.0001) more water than basalt after 1 hour of drying. On average limestone retains 88% of its max water capacity after one hour of drying whereas basalt is left with 41% of its max.

Abiotic conditions: soil collection and tests

The average soil pHs on basalt and limestone are 6.9 and 7.9, respectively. This difference is statistically significant (P=0.0002). The average pH buffering capacity is greater for limestone than basalt. On average 1.5 grams of limestone soils produced 10.3mL of gas whereas 1.5 grams of basalt soils produced 1.3mL of gas. This difference is statistically significant (P=0.0034). Lastly, the phosphorous concentration is significantly (P= 0.0016) higher on limestone than on basalt by 6 lb Acres/ 6" of soil. The average phosphate level on limestone soils was 16 lb Acres/ 6" of soil and 10 lb Acres/ 6" of soil on basalt soils. Table 1 summarizes the abiotic conditions on each substrate.

Field composition survey

A multivariate discriminant analysis of the community compositions on the two substrates showed that the centroids for each rock type and the circle around it, representing a 95% confidence in terms of the community belonging to a particular rock, were spatially separated [Fig. 3]. This means a

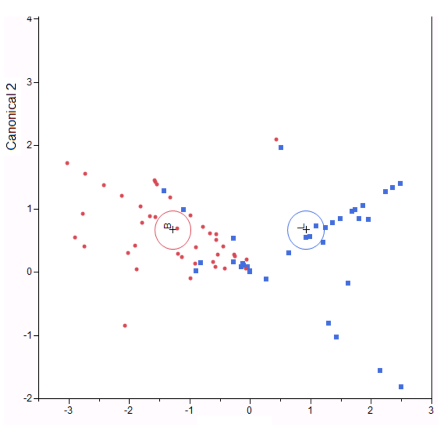

FIG. 3. MULTIVARIATE ANALYSIS SHOWING COMMUNITY COMPOSITION BETWEEN BASALT AND LIMESTONE. COMMUNITIES DIFFERENT BETWEEN SUBSTRATES

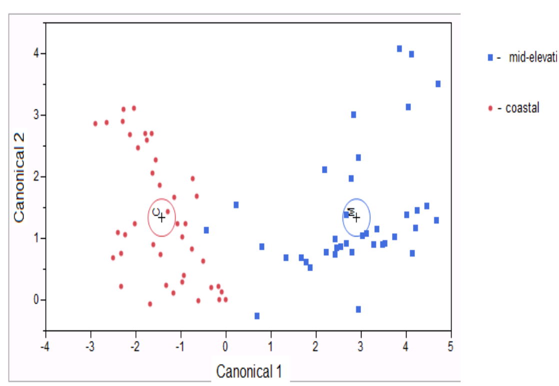

FIG. 4. MULTIVARIATE ANALYSIS SHOWING COMMUNITY COMPOSITION AT COASTAL AND MID ELEVATIONS. COMMUNITIES DIFFERENT BETWEEN ELEVATIONS

statistically significant difference in the community compositions on limestone and basalt. In addition a second multivariate discriminant analysis of the community compositions at coastal and mid elevations [Fig. 4] showed that the centroids for each elevation type and circle around it also did not overlap spatially. This means a statistically significant difference in community compositions exists between coastal and mid-elevation communities.

Looking at the species composition on basalt and limestone, some species are more abundant on one substrate while other species have similar abundances on either substrate [Fig. 5]. Performing a one-way ANOVA for each species with substrate as an effect, three species were shown to be statistically more abundant on basalt and two species on limestone. *Calymperes aongstroemii* (Bescherelle), *Ectropothecium sodale, and Taxithelium vernieri* (Verniersn) are more abundant on basalt (P values= 0.0016, 0.0012 and 0.0346, respectively). *Ectropothecium*

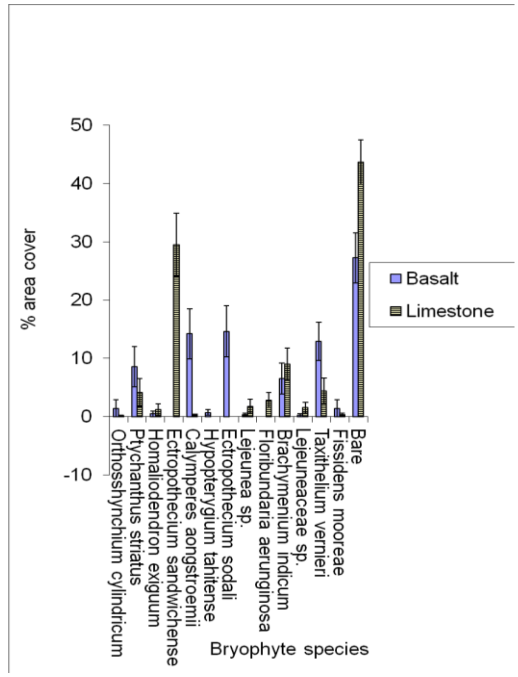

FIG. 5. SPECIES ABUNDANCE ON BASALT AND LIMESTONE. ERROR BARS ARE ONE STANDARD ERROR. DIFFERENT SPECIES HAVE DIFFERENT SUBSTRATE PREFERENCES.

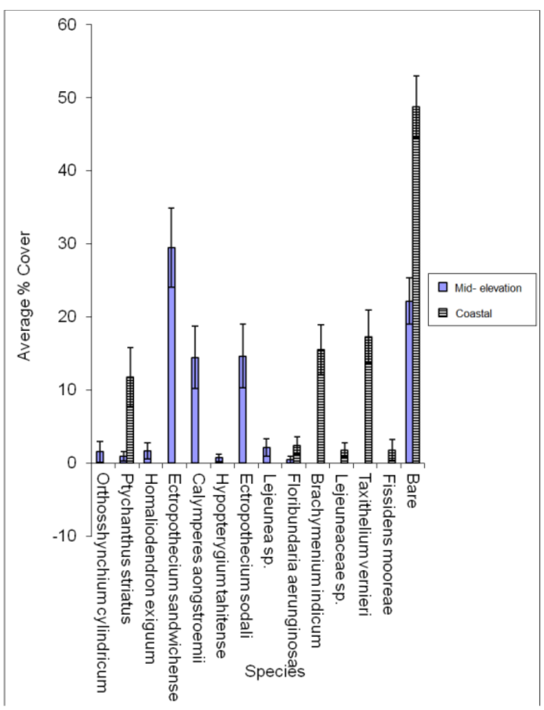

FIG. 6. SPECIES ABUNDANCE AT COASTAL AND MID ELEVATIONS. ERROR BARS ARE ONE STANDARD ERROR. DIFFERENT SPECIES HAVE DIFFERENT ELEVATION PREFERENCES.

sandwichense and *Floribundaria aerunginosa* (Mitten) are more abundant on limestone (P values= 0.0001 and 0.0253, respectively). Some species are also more abundant between elevations as seen in Fig. 6. *Ptychanthus striatus* (Lehm & Lindenb) Nees, *Taxithelium vernieri*, and *Brachymenium indicum* (Dozy & Molkenboer) Bosch & Lacoste are significantly (P values= 0.0097, 0.0001 and 0.0001, respectively) more abundant at coastal elevations. *Ectropothecium sandwichense*, *Calymperes aongstroemii*, and *Ectropothecium sodale* are significantly (P values= 0.0001, 0.0011, and 0.0012, respectively) more abundant at mid elevations. For a complete substrate and elevation preference evaluation for each species refer to appendix A. Interestingly, in mid elevations, limestone is significantly (P value =0.0006) more bare than basalt by an average of 21%. In coastal elevations, however, limestone is not significantly (P= 0.1477) more bare than basalt even though it is on average 13% more bare.

Growth manipulation: effects of substrate

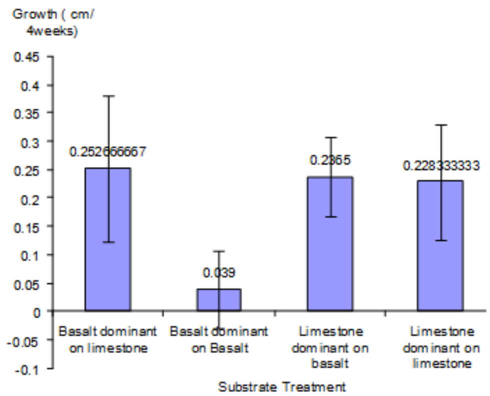

FIG. 7. EXPERIMENTAL GROWTH RATES OVER 4 WEEKS FOR BASALT AND LIMESTONE DOMINANT SPECIES ON BASALT AND LIMESTONE. ERROR BARS ARE ONE STANDARD ERROR. THE GROWTH RATES ARE NOT STATISTICALLY DIFFERENT UNDER ANY TREATMENT.

Although none of the bryophytes grown in lab had statistically (P value= 0.1731 when comparing basalt dominant species on different substrates and P value= 0.95 for the limestone dominant species on the two substrates) different growth rates, there was a general trend [Fig. 7]. The Basalt dominant species in nature grew 6.4 times more on limestone than on basalt. The basalt dominant species also experienced some negative growth (decrease in length) on basalt. On average the limestone dominant species, in nature, grew 0.0082 cm more on basalt than on limestone.

DISCUSSION

Substrate abiotic conditions

The physical and chemical properties associated with each substrate examined were different. Firstly, water holding capacity was greater on limestone than on basalt by 13.7 times with limestone holding 0.0992 grams more water per gram of rock than basalt. This difference can be explained by limestone's more porous nature (McWorter and Sunada 1977) allowing it to have a greater volume to retain more water. Also, after 1 hour of drying, limestone retained 90% of its maximum water holding capacity compared to 40% for basalt. This indicates that most of the water in limestone is held inside the rock, making it difficult to evaporate the water. For basalt, however, most of its water is on the surface where it is easily evaporated. Because limestone is able to hold onto more water for a longer time than basalt, the soils on limestone will remain more moist than soils on basalt making moisture differences a potential factor influencing a specie's substrate preference. For example, during dry seasons, this extra moisture on limestone could be vital for the survival of some species that have low desiccation tolerance. Secondly, the basalt soils were more acidic than the limestone soils by 1.8 pH units. This is likely due to the presence of calcium carbonate on limestone soils buffering against acidification. In fact, the gas measurements support this by showing that 1.5grams of limestone soils produced, on average, 9mL more gas when exposed to hydrochloric acid compared to basalt soils. It is worth noting, however, that the buffering capacity of basalt soils is not zero. Basalt does contain minerals and metals like iron, magnesium and calcium that can undergo dissolution and react with strong acids (Golden et al. 2005). In forests, soils are naturally acidified by decaying litter (Tamm and Hallbäcken 1988) thus if a substrate has a greater potential to buffer against this, it would result in a higher pH. Finally, phosphorous levels were 3ppm higher on limestone soils than basalt soils. This can be explained by the fact that phosphates have different solubilities depending on soil pH and chemical interactions with minerals (Bailey 1996). For example on the one hand, although phosphates can become bioavailable by reacting with aluminum and iron (Busman 1997), minerals typically more abundant in acidic soils (like basalt), these phosphates tend to be less soluble, and hence less bioavailable to plants. On the other hand, phosphates fixed by calcium (Busman 1997), typically more abundant in alkaline soils (like limestone), are more soluble and hence more bioavailable to plants. This explains why phosphate levels might have been higher in limestone soils versus basalt soils.

Bryophyte composition

The physical and chemical properties associated with each substrate did translate into different bryophyte communities on each substrate. For example, the spatial separation of the two centroids in the discriminant analysis shows that the communities found on each substrate type is very different. The DF (misclassified) substrate was 11 out of 84 samples indicating that 87% of the rocks had a community composition on them that was relatively similar to another community on the same type of rock. This means that communities on basalt are more similar to ones on other basalts than they are to those on limestone and vice versa. A second discriminant analysis looking at communities between coastal and mid elevations revealed that not only are communities very different between substrates but they are also very different between elevations. In fact a DF (misclassified) of 3 out of 84 shows that 97% of the time a sample can be correctly predicted to be at a certain elevation based on its community composition alone. In other words this means that the community composition was very distinct between coastal and mid elevations. This was verified by looking at the strong spatial separation between the two centroids indicating that the multivariate average communities at coastal and mid elevations were very unique. The exact species composition of these communities was determined using 1-way ANOVAs looking at substrate and elevation effects, separately, for each species. This showed the substrate and elevation preferences for each species based on the field survey. For example, species like *Calymperes aongstroemii* and *Ectropothecium sodale* prefer basalt at mid- elevation forests whereas a species like *Ectropothecium sandwichense* prefers limestone at mid-elevation forests. *Taxithelium vernieri* prefers limestone at coastal forests. *Orthosshynchium cylindricum* (Zander), *Ptychanthus striatus*, *Homaliodendron exiguum* (Bosch & Lacoste) Fleischer , Lejeuneaceae sp., *Fissidens mooreae* (Whittier & Miller), *Lejeunea* sp., *Brachymenium indicum* are species that can be found on both substrates without a preference (P values > 0.05) for either type, even though each may have a different elevation preference. *Floribundaria aerunginosa* is the only species that is found on both coastal and mid elevations. It also does not have a significant difference in abundance between the two elevations. Although one-way ANOVA tests for each species, for substrate and elevation effects, does provide statistically significant ecological information for some species, it does not do so for all. For example although a species like *Hypopterygium tahitense* (Aongstrom) was only ever found on basalt and at mid-elevations for this study it did not have a statistical "preference" for either substrate or elevation because its abundance was too low to be statistically significant. This means *Hypopterygium tahitense* was a very rare species and more data is needed on it to determine its ecological preferences if it has one. Despite these short comings, the results have yielded five substrate preferred species that may be used as potential bioindicators: these include *Calymperes aongstroemii, Ectropothecium sodale*, and *Taxithelium vernieri* for "basalt-like" conditions and *Ectropothecium sandwichense* and *Floribundaria aerunginosa* for "limestone-like" conditions.

These species on Mo'orea add to our knowledge of factors that influence bryophyte distribution and provide credibility to the idea of using bryophytes to assess abiotic conditions like acidity, phosphate and moisture levels. The distribution of these five species by substrate abiotic preference is consistent with other bryophyte distribution patterns around the world. For example, Tyler (2005) showed that pH and phosphate levels influenced bryophytes diversity in Swedish sand steppe vegetation habitats. He showed that as phosphate levels increased there was a negative correlation with bryophyte diversity indicating that species have different phosphate tolerances. Another example of bryophytes responding to abiotic factors is seen in the Hawaiian montane forests where certain species preferentially grow on high phosphorous trees (Benner 2011). Based on these studies of how phosphorous influences species distribution in other parts of the world and the results indicating different phosphate levels between limestone and basalt, it is reasonable to hypothesize that differences in phosphate levels might be responsible for the unique community compositions observed on the two substrates on Mo'orea. In addition to phosphate differences, water availability differences between the substrates could also be an important factor for distribution. For example, Vincke *et al*. (2004) showed that some bryophyte species like *B. integrifolia* and *S. uncinata* have a geographic distribution that is correlated with different moisture levels. Because the substrates have such different water holding capacities, it is also possible that the species found on each substrate is there because of the differences in moisture. It is currently unclear, however, which abiotic factors are most important in governing the distribution of these species. Further research into the physiology of these species will offer insight in this area.

In terms of looking at the overall bare coverage on the two substrates, it is interesting to point out that the bare cover was statistically (Prob>F= 0.0006) greater on limestone versus basalt by 21% at mid-elevations but not at coastal elevations. This could be due to the fact that limestone has only been introduced to the mid-elevations for 300 years and is still a very foreign rock at these elevations compared to the basalts which have been there for thousands of years. Consequently, the bryophytes at mid-elevation have had more time to adapt to living on basalt than on limestone which would explain the greater diversity and coverage on basalt and the relative barrenness on limestone at this elevation.. In the coast, however, the bare coverage is not statistically different (Prob>F= 0.1477) possibly indicating that the limestone has been present for much longer and consequently the bryophytes there have had more time to adapt to living on that substrate.

Growth experiment

The results of this experiment, which showed that substrate type does not directly affect the growth rates for two species (*Ectropothecium sodale* and *Ectropothecium sandwichense*) , refutes the hypothesis that substrate, alone, would dictate bryophyte distribution. For example, the growth rate of *Ectropothecium sodale* (the basalt dominant species) actually grew at a slower rate on basalt than on limestone by about 0.213 cm/ 4 weeks. This indicates that although substrate abiotic factors may be important for influencing the distribution of some species by providing an environment in which they can thrive, biotic factors might also be very important. In nature *Ectropothecium sodale* grows together with other bryophytes like *Calymperes aongstroemii*. *Calymperes aongstroemii* could be facilitating the growth of *Ectropothecium sodale* by preventing soil erosion or helping to retain moisture (Bates *et al*. 2005) because, as the abiotic results showed, basalt is not good at retaining moisture. Thus, the absence of *Calymperes aongstroemii* could have resulted in *Ectropothecium sodale*'s poor growth.

Another interesting result from this experiment is that *Ectropothecium sodale* and *Ectropothecium sandwichense* both showed that they could, physiologically, grow on the other's substrate when given an excess of water on a daily basis. If they can tolerate both substrates and assuming that water is in excess in rainforest habitats, why do these two species 1) have a substrate preference and 2) why are they not found at coastal elevations? Possible explanations for this include elevation associated abiotic factors like shade, humidity, average rainfall, and salinity (Lee & Roi 1979) that are different between elevations which may limit their geographic range even though there are suitable substrates in coastal areas. In addition other factors like dispersal or biotic factors could be in play. For example even though a species might be able to, physiologically, thrive on a substrate it might have no means of dispersing to it thus restricting its distribution to only mid-elevations. In addition, some bryophyte predators (Smith *et al*. 2008) or competitive plants might only exist at lower elevations or only on certain substrates which may prevent the establishment of higher elevation species at lower elevations or the establishment of a species from one substrate to another.

CONCLUSIONS

In conclusion, the abiotic results support the hypothesis that soil pH, buffering capacity, phosphate levels and substrate water retention ability is different for limestone and basalt by indicating that limestone is more basic, has greater buffering capacity, phosphate levels and substrate water retention ability than basalt. Biologically, this translated into different community compositions between substrates and between elevations. 5 bryophyte species showed a statistically significant substrate preference and many showed an elevation preference. *Ectropothecium sandwichense* and *Floribundaria aerunginosa* showed a limestone preference whereas *Calymperes aongstroemii*, *Taxithelium vernieri*, and *Ectropothecium sodale* showed a basalt preference. The 5 bryophyte species that are tightly associated with a substrate may be used as indicators of "limestone-like" and "basalt-like" conditions thereby bypassing the need for abiotic tests. The ability to quickly detect habitat change as a result of substrate addition is directly important to the people of Mo'orea, especially when limestone is currently being used as fill material in road construction up to sites in the mid-elevation forests. The biological hypothesis that the communities would be completely different between substrates and elevations is only partially supported, however, because some species had neither a substrate nor an elevation preference like *Orthosshynchium cylindricum*, *Homaliodendron exiguum*, *Hypopterygium tahitense*, *Fissidens mooreae*, *Lejeunea* sp., and Lejeuneaceae sp. This could, however, be due to insufficient field data on these species. More data on these species might yield a preference. For now, they are considered more generalist species. Experimentally, *Ectropothecium sodale* and *Ectropothecium sandwichense* was found to be physiologically able to grow on both substrates indicating that biotic and elevation associated effects might also contribute to the distribution of bryophytes on Mo'orea. Further investigation into the relationships between pH, nutrient levels and water availability and how this affects bryophyte physiology will contribute to the understanding of which of these parameters is most important towards affecting the distribution of these plants. This information would allow locals, scientists and planners to use the presence and abundance of these plants as a proxy for specific abiotic conditions in the future.

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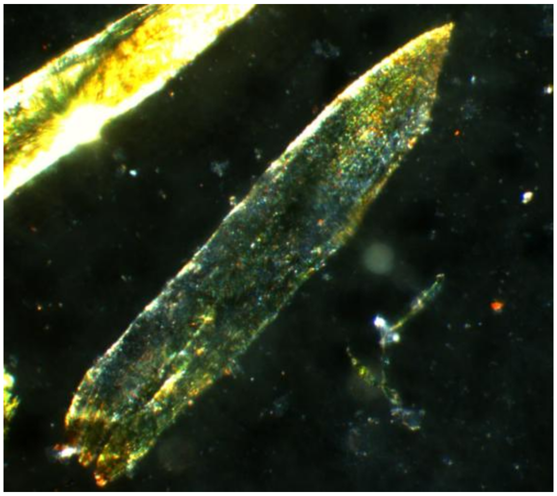
APPENDIX A

The chart below catalogs the site(s) each species was present and the substrate(s) each were found on. 1 way ANOVAs were done for each species, against substrate and elevation, separately, was used to determine if the distribution of that species was significantly correlated with substrate or elevation. If it was, then that species "preferred" a certain substrate or a certain elevation.

Species	Site(s)	Substrate (s)	Rock Pref?	Elevation Pref?
Orthosshynchium cylindricum	3	Basalt and limestone	No	No
Ptychanthus striatus	2,3,4,5,6	Basalt and limestone	No	Yes, coastal preference. P= 0.0097
Homaliodendron exiguum	*1,3*	Basalt and limestone	No	No
Ectropothecium sandwichense	*1,2,3*	Limestone	Yes, limestone P= 0.0001	Yes, mid P=0.0001
Calymperes aongstroemii	*1,2,3*	Basalt and limestone	Yes, basalt P= 0.0016	Yes, mid P= 0.0011
Hypopterygium tahitense	*2*	Basalt	No	No
Taxithelium vernieri	*4,5,6*	Basalt and limestone	Yes, basalt P= 0.0346	Yes, coastal P= 0.0001
Brachymenium indicum	*4,5,6*	Basalt and limestone	No	Yes, coastal P=0.0001
Fissidens mooreae	*5,6*	Basalt and limestone	No	No
Ectropothecium sodale	*1,2,3*	Basalt	Yes, basalt. P= 0.0012	Yes, mid P=0.0012
Floribundaria aerunginosa	*3,5*	Limestone	Yes, limestone P=0.0253	No
Lejeunea sp.	*2,3*	Basalt and limestone	No	No
Lejeuneaceae sp.	*4,5*	Basalt and limestone	No	No

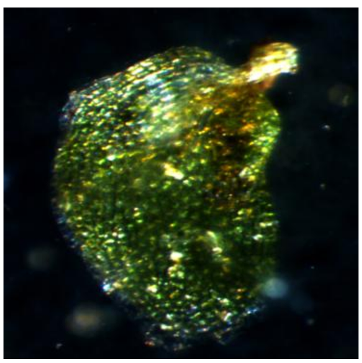
APPENDIX B

Below are pictures of each of the bryophytes that were studied in this paper.

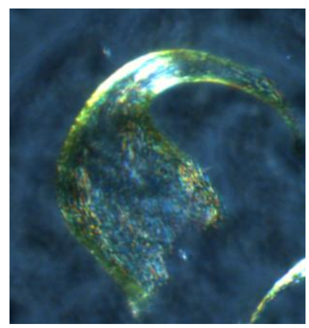


Orthosshynchium cylindricum

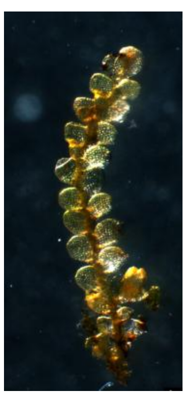
Fissidens mooreae



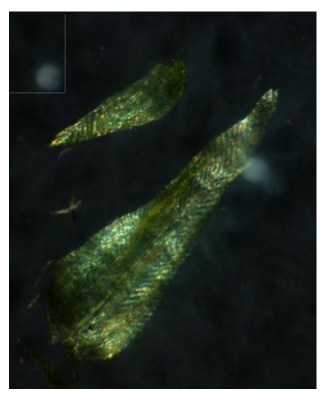
Lejeuneaceae sp



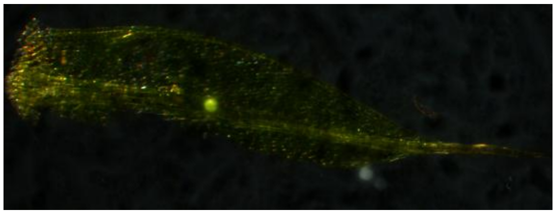
Ectropothecium sodale



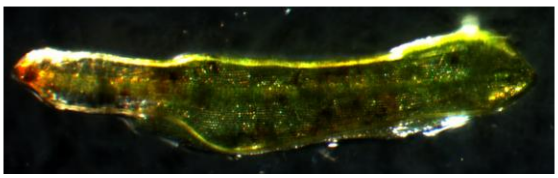
Lejeunea sp.



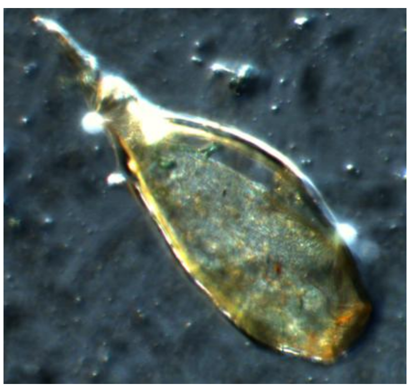
Floribundaria aerunginosa



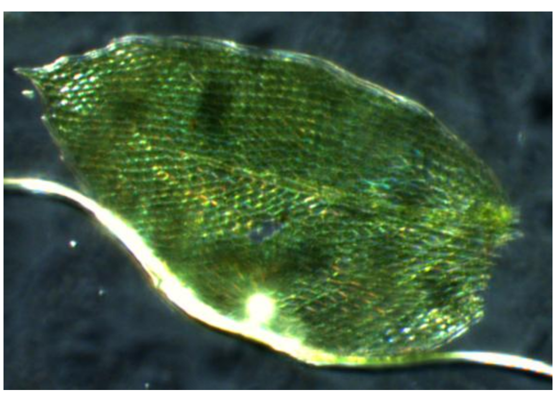
Brachymenium indicum



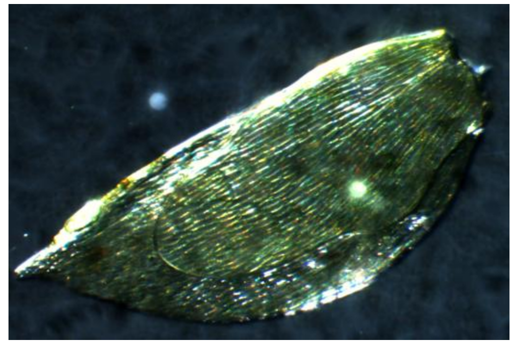
Calymperes aongstroemii



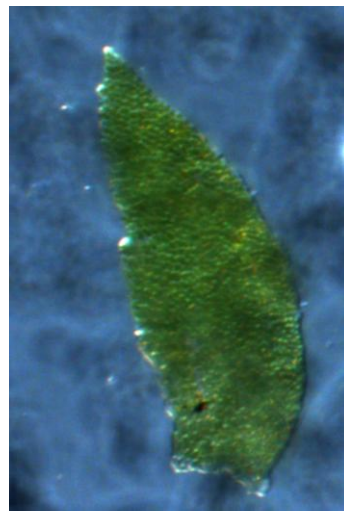
Taxithelium vernieri



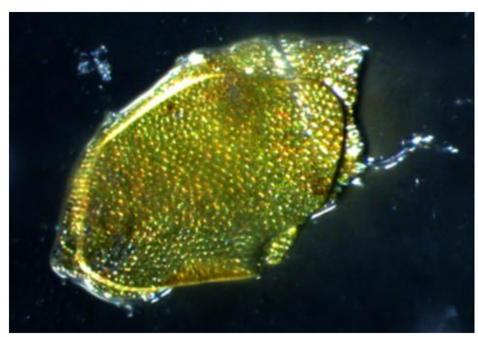
Hypopterygium tahitense



Ectropothecium sandwichense



Homaliodendron exiguum



Ptychanthus striatus