

Adaptive Traits and Community Assembly of Epiphyllous Bryophytes

By

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Abstract

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Leaf surfaces of tropical vascular plants provide homes for diverse groups of organisms, including epiphyllous (leaf-colonizing) bryophytes. Each leaf harbors a temporally and spatially discrete community of organisms, providing an excellent system for answering some of the most fundamental questions in ecology and evolution. In this dissertation, I investigated two main aspects of epiphyllous bryophyte biology: 1) adaptive traits of bryophytes to living on the leaf surface, and 2) community assembly of epiphyllous bryophytes in space (between-hosts) and time (succession).

For the first part, I used published trait data and phylogeny of liverworts in family Lejeuneaceae to demonstrate that only the production of asexual propagules appeared to evolve in response to living on the leaf surface, while other hypothesized traits did not have correlated evolution with epiphyllous. The second portion dealt with the assembly of communities among different host types. In this part, I identified communities of epiphyllous bryophytes from the same set of three hosts across the gradient of water deficit fluctuation, as represented by the daily range of vapor pressure deficit (VPD) on the island Moorea, French Polynesia. Dissimilarity of epiphyllous communities among host types (beta diversity) increased with the increasing VPD range, suggesting that assembly of bryophyte community may depend on microclimate fluctuation. In the last portion of this dissertation, I investigated temporal changes of epiphyllous communities on *Inocarpus fagifer*, using chronosequence and long-term observation of tagged leaves in the field. Data from both approaches showed significant changes in abundance, species richness, and composition over time. These successional changes, however, did not follow any single trajectory, resulting in divergent communities among leaves of older age. Together, the results from this dissertation work improve our understanding of fundamental biology of epiphyllous bryophytes and allow future researchers to use this system to answer broader questions in ecology and evolution.

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Preface

As a native of a tropical country, I was somehow completely unaware of the fact that bryophytes could grow on leaf surfaces. It was not until January 2009 when I roamed around a forest in southern Thailand looking for my dissertation topic that I encountered so many of these peculiar communities. So called “epiphyllous bryophytes,” these tiny plants occur on leaves of various vascular plants – from selaginella to seedlings of angiosperms. A closer look at these bryophytes told me that their existence on this habitat form was far from being accidental. They formed a solid mat and reproduced profusely on rather unstable, short-lived surfaces of leaves. Trained as a community ecologist, I was intrigued by their ubiquitous, but patchy distribution across humid forests, as well as the idea of using these spatially well-defined communities as a study system for larger questions in ecology. At that time, I thought that something this unique must have been studied to death. I was dead wrong.

Epiphyllous bryophytes never escape keen eyes of tropical biologists. Since the first official report at the end of 18th century, they continue to fascinate people who come across their existence. They have added to exoticism and mysteries of tropical diversity. However, the majority of the works have focused on figuring out their taxonomy, and surprisingly not much else. We know that 95 percent of epiphyllous bryophytes belong to the family Lejeuneaceae – a taxonomically challenging group of over 1,000 liverwort species. While this group has made a career for many bryophyte systematists, ecologists are not so thrilled by the prospects of identifying these plants, let alone trying to understand their ecology and evolution. So far, we have speculated on what allows them to thrive on leaves and produced only have some scattered data on how an epiphyllous community is assembled in space and time. Many hypotheses and observations have been made. Only a few have actually been tested.

Through subsequent trips to the tropics, I joined previous generations of tropical botanists in making casual observations about epiphyllous bryophytes. In a cloud forest of Malaysia, epiphylls were everywhere, covering all types of leaves. A few hundred meters down the elevation, they suddenly become harder to find, only occurring on certain types of leaves. The forests were similar. The only difference seemed to be the amount of water. To determine what was going on, I brought a few leaf samples back with me, only to become even more confused. Leaves from the same plant seemed to have different communities of bryophytes. All these variations! What could explain all them? Host specificity? Succession? Speculations could go on, but in a spirit of a doctoral student, I decided to test some hypotheses.

This dissertation is an attempt to learn about this group of bryophytes more systematically by testing some specific hypotheses regarding their adaptation and assembly. I take advantages of modern analytical tools and current conceptual frameworks in ecology to formulate this study. The first chapter on adaptive traits challenges a long-standing hypothesis that epiphyllous bryophytes possess a suite of morphological traits, specifically adapting to living on leaves. Using phylogenetic comparative analyses, I show that not all trait-epiphyll correlations are the results of adaptation to the epiphyllous habit, and only the production of asexual propagules seems to be the only real adaptive trait. The second chapter re-evaluates host specificity of epiphyllous bryophytes through the conceptual lenses of beta diversity and demonstrate that their distribution among host types may depend on microclimate fluctuation. Finally, the last chapter takes another critical look at temporal changes, or succession, of communities, and demonstrates that succession of leaf may be more complex than originally thought. Together, this body of work reveals a highly dynamic nature of epiphyllous communities that respond rapidly to changes

in conditions and substrate availability, making them a potential candidate for an excellent study system for broader questions in ecology and evolution.

The work is by no means complete. Many more hypotheses about mechanisms behind observed patterns in epiphyllous communities remain untested. I hope that the findings from this work will enable and encourage future researchers (including myself) to dig deeper in ecology and evolution of epiphyllous bryophytes. If nothing else, I believe I have turned natural history of these organisms into something testable and solved a few tropical mysteries – one dissertation at a time.

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CHAPTER 1:

Asexual Propagules As An Adaptive Trait For Epiphyllly In Tropical Leafy Liverworts (Lejeuneaceae)

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ABSTRACT

Many links between form and function are described in the context of adaptation. Several morphological and life-history traits in the leafy liverwort family Lejeuneaceae (Marchantiophyta) have been hypothesized to be adaptations for living on the surface of leaves of vascular plants (epiphyllly). There have been, however, no rigorous tests of these hypotheses. Using a recently published phylogeny of Lejeuneaceae and trait data from published monographs, I tested the correlations of putative adaptive traits with the incidence of epiphyllly. Both cross-species and phylogenetic-based analyses of trait data were performed to distinguish the patterns of shared evolutionary history from independent origins of putatively adaptive traits. The rates of transitions between different combinations of character states were also calculated to determine whether traits were more likely to evolve in the presence of epiphyllly. Only one trait, production of asexual propagules, was correlated with epiphyllly in the phylogenetic-based analysis. The rate of transition to asexual propagules was also significantly higher in the presence of epiphyllly. Other traits correlated with epiphyllly appeared to be the results of shared evolutionary history among sister taxa and therefore not due to adaptive evolution. The present study distinguished production of asexual propagules from other traits as a key adaptive response to living on the leaf surface. No other putative “adaptive” traits to epiphyllly showed evidence of being specific adaptation to epiphyllly. The results highlight the importance of phylogenetically controlled methods in determining an adaptive function of traits.

Key words: epiphyllly; leafy liverwort; Lejeuneaceae; Pagel’s test; trait correlation.

INTRODUCTION

Adaptation stands as one of the most intriguing and perhaps the most challenging ideas in evolutionary biology. The concept has been frequently, but loosely discussed in the context of correlations between organisms’ traits and their environment, with ad hoc explanations of their function (Gould and Lewontin, 1979). Not all trait–environment associations, however, can be explained by adaptation. In the strictest sense, for a trait to be an adaptation, it must be derived in response to a particular emergent environment (Coddington, 1994). In many cases, the trait–environment correlation is a result of shared evolutionary history and may or may not be adaptation to that particular environment. It is only recently that advances in phylogenetics and comparative methods have allowed biologists to test the hypotheses of adaptation under stricter criteria and identify the cause of trait–environment correlations (Harvey and Pagel, 1991). If a trait exhibits an association with environment in a traditional cross-species analysis, but fails to

produce a significant result in a phylogenetic-based test, then it is likely that the trait–environment association is the result of shared evolutionary history of closely related taxa, which possess similar traits. Our ability to properly interpret the evolution of traits and adaptation has become increasingly important as we attempt to predict species’ responses to rapidly changing environments (Chevin et al., 2010).

Epiphyllous liverworts have long captured the interest of tropical ecologists and botanists, because of their unique habitat and the presumed adaptations necessary for surviving in that habitat (Richards, 1984). Unlike more typical substrates for liverworts, leaves are themselves living entities—relatively ephemeral and subject to constant changes of humidity and chemical composition of the surface. Only a very limited number of taxa are found growing on leaves and presumably possess certain traits (morphological, ecological, life-history), which allow them to colonize and persist in this transient environment. Bryologists have proposed many morphological and life-history traits that they attribute to the liverwort’s ability to inhabit the surface of leaf (Gradstein, 1997; Schuster, 1988; Zhu and So, 2001). In this paper, this ability is referred to as “epiphyllly.”

Proposed adaptations to epiphyllly have mainly been related to the liverwort’s ability to (1) retain water, (2) adhere to the leaf surface, or (3) reproduce and disperse propagules rapidly (Zhu and So, 2001). Trait associations with water retention include inflated water sacs (lobules), papillose cells, and imbricate leaves (Proctor, 1990) (**Fig. 1.1**). Flattened perianths, appressed stems and secondary rhizoid discs are associated with the ability of the liverworts to adhere to leaves (Winkler, 1967; Zhu and So, 2001). Monoicy (both sexes on a single gametophytic individual) and specialized asexual propagules are assumed to be important for short-lived and dispersal-limited epiphyllous liverworts, because of the ephemeral nature of the leaves (Schuster, 1988; Zartman and Nascimento, 2006). Last, neotenic features—having juvenile characters in a mature plant—are believed to be associated with epiphyllly, as many neotenic genera of the Lejeuneaceae, especially those of the *Tuyamaella-Cololejeunea* lineage, are typically epiphyllous (Gradstein et al., 2003; Wilson et al., 2007b). These associations, however, are based solely on anecdotal observations made in previous taxonomic studies and have not been quantitatively tested for their adaptive significance. It is possible that these “adaptive” traits are, in fact, exaptations (Gould and Vrba, 1982), having evolved in other context, but contributing currently to epiphyllly.

Leafy liverworts in the Lejeuneaceae provide a valuable system for the study of trait evolution and correlation in epiphylls, because 95% of the over 500 recognized epiphyllous liverworts belong to multiple lineages in this family (Gradstein, 1997), with the majority of species in the family being epiphytic (including non-epiphyllous growth on twigs and bark). Also, a robust phylogenetic study of evolutionary relationship in this family has recently been completed (Wilson et al., 2007a). Incorporating phylogenetic information in a comparative analysis addresses the issue of non-independence of data points, which may arise from conservatism of traits among species derived from a common ancestor (Felsenstein 1985; Harvey and Pagel, 1991). Therefore, by considering phylogenetic relationships among non-epiphylls and epiphylls in this group, it is possible to formally test whether traits presumably associated with epiphyllly are adaptations in the sense of Coddington (1994).

The objective of the present study was to determine whether proposed adaptive traits were an adaptation for epiphyllly in the strict sense (i.e., derived in response to a particular emerging environment). More specifically, the present study aimed to answer the following questions: (1) Are putatively “adaptive” morphological traits actually correlated with epiphyllly?

(2) If so, did the correlations arise from shared history of taxa (i.e., trait conservatism) or independently in response to the presence of epiphylls? (3) Is the rate of acquisition of these traits higher in the presence of epiphylls?

METHODS

Phylogeny — The phylogeny of Lejeuneaceae was reconstructed using the methods and GenBank sequences reported by Wilson et al. (2007a). The analysis contained representatives of 131 taxa in Lejeuneaceae and three outgroup taxa from Jubulaceae and Nipponolejeuneaceae (**Table 1.1**). GenBank sequences from *rbcL*, *psbA*, *trnL-F*, and *nrITS* regions were concatenated and subjected to a Bayesian phylogenetic analysis in the program MRBAYES (Huelsenbeck and Ronquist, 2001), following the methods of Wilson et al. (2007a). The 4900 trees remaining in the posterior probability space after the burn-in were used in the subsequent analyses to address the issues of phylogenetic uncertainty (see *Phylogenetic correlation analysis*). The R packages *ape* and *geiger* and the program Mesquite were used for tree manipulation and illustration (R Development Core Team, 2010; Paradis et al., 2004; Maddison and Maddison, 2009; Harmon et al., 2009).

Liverwort traits — Based on two previous reviews of adaptations of epiphyllous bryophytes (Schuster, 1988; Zhu and So, 2001), eight characters were selected for the present study: (1) stem size, (2) sexuality, (3) leaf position, (4) cell surface, (5) degree of lobule inflation, (6) degree of perianth inflation, (7) presence of asexual propagules, and (8) presence of neotenic feature (**Fig. 1.1**; **Table 1.2**). “Epiphylls” was defined in two ways for the analyses. “Common epiphylls” referred to the taxa that are frequently found on leaves. “All epiphylls” referred to all taxa known to colonize the surface of leaves at least occasionally. This definition included all the taxa under “common epiphylls” and other taxa reported as “occasional epiphylls” (Gradstein, 1997) (**Table 1.1**). Parsimony ancestral state reconstructions of epiphyll traits on the studied phylogeny revealed 13 parsimony steps for “all epiphyll” and 9 steps for “common epiphyll” (results not shown; **Appendix 1**). Trait data for each taxon were collected from published monographs and descriptions (see **Table 1.1**). For a taxon with no description, the description of one of its synonym reported in the TROPICOS database (TROPICOS.org, 2009) was used. Six specimens in the study by Wilson et al. (2007a) were only identified to the genus level. In these cases, genus level characters from the literature were used. When trait data were not available from published literature of any kind, the values were coded as missing data.

To generate a proxy character for stem size, three stem traits (stem diameter in millimeters, number of cortical cells, and number of medullary cells) were analyzed using principal components analysis (PCA). The published descriptions generally report these stem traits as a range of values. For all analyses, the midpoint values of the published range were log-transformed prior to the PCA. The first principal component (PC1), which explained 91% of variation, was used for “stem size” values. The values were then discretized into two states, small and large, using the median of PC1 scores. The remaining traits were directly coded as discrete characters with two character states (**Table 1.2**). For the bryophyte sexuality trait, monoicous, autoicous, paroicous, and cladautoicous species were coded as monoicous, and the rest of the taxa as dioicous. The leaf position of liverworts is either imbricate (proximal leaf edge overlaps with the distal edge of the leaf below it), or distant (majority of the edges of leaves do not overlap). For the purpose of this study, taxa described as subimbricate or contiguous were also

coded as imbricate to be consistent with the hypothesis that the proximity of leaf lobes helps retain water in the plant.

For the cell surface, any taxon with papillose, or mammillose cells was coded as papillose, and the rest as smooth. For the degree of lobule inflation, taxa with inflated, or swollen lobules were coded as inflated and the rest as flattened. For perianth inflation, any taxon with the description of an inflated or terete perianth was coded as inflated, and a taxon with the description of a flattened or dorsiventrally flattened perianth was coded as flattened. When the inflation of the perianth was not mentioned, perianths with three or more keels were coded as inflated, and those with two or fewer keels were coded as flattened. Specialized asexual propagules for taxa producing gemmae or cladia were coded as present, and coded as absent for taxa without these structures. The scoring of neotenic features followed the methodology of Gradstein et al. (2003), which was based on the presence of pendular sequence of leaf and underleaf on mature stems (gametophyte character 19 in the reference).

Secondary rhizoid discs, or adhesive discs, are one of the most prominent features of epiphyllous taxa, as they are reported to only occur in typical epiphylls and never in the facultative ones (Gradstein, 1997; Winkler, 1967). However, this trait was excluded in this study, because data on the presence of secondary rhizoid discs were rarely reported in taxon descriptions and thus could not be collected systematically.

Cross-species analyses — Correlations between epiphyllly and traits commonly associated with epiphyllly were identified using traditional cross-species analyses, which treated character state for each trait by taxon as a single, independent data point, under two definitions of epiphyllly (“all epiphylls” and “common epiphylls”). Pearson’s χ^2 tests were used to determine whether epiphyllous taxa were more likely to possess the epiphyllous character state. Both tests were performed in the program R (R Development Core Team, 2010). Taxa with missing data were excluded from the analysis.

Phylogenetic correlation analysis — Correlations between each of the eight traits and epiphyllly were tested using the Markov chain Monte Carlo (MCMC) approach in the Discrete module of the program BayesTraits (Pagel, 1994; available from www.evolution.rdg.ac.uk). The amount of change between subsequent sampling iterations controlled by the `ratedev` option was altered, so that the acceptance rates by the Metropolis–Hasting algorithm were globally between 20% and 40% (Pagel and Meade, 2006). Similar to the cross-species analysis, the phylogenetic correlations were analyzed, using both definitions of epiphyllly.

For each correlation analysis, two separate chains were run using two models: an independent model (*I*) and a dependent model (*D*). The independent model assumes that the rate of change between states in one character does not depend on the state of another character and therefore only estimates four parameters for the transition rates among four possible combinations of character states (**Table 1.3**). The dependent model, on the other hand, assumes that the rate of change between states of a character depends on the state of the other character and thus estimates eight transition rates among the four combinations of character states (**Table 1.3**; Pagel 1994). If a trait and epiphyllly are correlated, the dependent model will have a higher likelihood than the independent model. The Bayes factor (BF) was used to compare the performance of these two competing models (Pagel and Meade, 2006); BFs were expressed as 2 times the difference between the harmonic means of the log-likelihood of model *D* and the log-likelihood of model *I*. A positive value of $BF > 3$ provides support for the dependent model and therefore correlation between the trait and epiphyllly (Pagel and Meade, 2006).

For each significant correlation between a trait and epiphyllly, I further tested whether the acquisition rate of that trait depended upon the presence of epiphyllly or vice versa. If the acquisition rate of that trait depends on the epiphyllous state ($q_{13} \neq q_{24}$, **Fig. 1.2**), then it is likely that the trait evolved in response to the presence or absence of epiphyllly and can thus be considered as an adaptation (Pagel 1994; Devos et al., 2011). To test this hypothesis, the two acquisition rates of the trait (q_{13} , q_{24}) in the dependent model (D) were restricted to be equal. Then, the likelihood of this restricted model was compared to that of the dependent model (i.e., $q_{13} \neq q_{24}$) to determine the best-fit model, using BF's (Pagel and Meade 2006). In this case, the BF was expressed as 2 times the difference between the harmonic means of the log-likelihood of model D and the log-likelihood of the restricted model. For q_{13} and q_{24} to be different, the BF must be three or greater.

Alternatively, if the transition rate to epiphyllly depends on the state of the other character ($q_{12} \neq q_{34}$), the trait is considered an exaptation in the sense of Gould and Vrba (1982). Another model with two transition rates to epiphyllly of the dependent model were restricted to be equal ($q_{12} = q_{34}$) was constructed, and its likelihood was compared to that of the dependent model using the same method as above.

RESULTS

Cross-species comparisons — Six of eight traits were significantly correlated with epiphyllly (**Table 1.2**). With the “all epiphyll” definition, epiphyllous taxa were more likely to have inflated lobules, smaller stems, neotenic features, and less likely to have imbricate leaves (Pearson's χ^2 , $P = 0.006$). Under the “common epiphyll” definition, the presence of cell papilosity and asexual propagules were also significantly correlated with epiphyllly, but the correlation with inflated lobules was not recovered (Pearson's χ^2 , $P \leq 0.02$).

Phylogenetic-based comparisons — There was no support for correlated evolution between epiphyllly and six of eight traits (sexuality, cell surface, lobule, perianth, neotenic features), regardless of the definitions of epiphyllly (BF ≤ 0.62 , **Table 1.4**). Leaf position did not evolve in a correlated fashion with “common epiphyll” (BF = -4.56), and there was no evidence for either model in the analysis with “all epiphyll” (BF = 1.39).

Only the analysis of asexual propagules and common epiphyll showed evidence for correlated evolution (BF = 3.08, Table 4). The comparison between the dependent model and the first restricted model ($q_{13} = q_{24}$) also indicated that the transition rate to asexual propagules was higher in the epiphyllous state ($q_{24} = 66.97$, $q_{13} = 1.02$, BF = 15.8, **Fig. 1.2**). The other comparison with the second restricted model ($q_{12} = q_{34}$) showed that it was more likely that the transition rates to common epiphyll were equal in both presence and absence of asexual propagules (BF = -8.62 , **Fig. 1.2**).

DISCUSSION

Presence of asexual propagules was the only trait significantly correlated with common epiphyll in both the cross-species and phylogenetic-based analyses. The higher rate of transition to having asexual propagules in the presence of common epiphyll (**Fig. 1.2**) also suggests that asexual propagules could be considered an adaptation for epiphyllly.

This result is consistent with the previous hypothesis that the production of asexual propagules is an adaptation to a rapidly changing environment. Asexual propagules have been shown to be more tolerant of wider ranges of temperature and humidity, as well as more likely to form a new gametophyte than spores (Mishler and Newton, 1988; Proctor et al., 2007). Leaves—the substrates of epiphyllous bryophytes—are highly dynamic in terms of water availability, temperature, and life spans (Gradstein, 1997; Zartman, 2004). Therefore, ability to reproduce asexually can provide a selective advantage for a commonly epiphyllous liverwort.

Interestingly, the correlation between asexual propagules and epiphyllly was not significant under the “all epiphyll” definition. The different results under the two definitions suggest that occasional epiphylls might not rely on asexual propagules as much as the common epiphylls. Occasional epiphylls may not have any specific adaptive traits to exploit the leaf surface because many generalist liverworts and certain mosses can be found on the leaves in very wet areas (Pócs, 1996). It is also possible that occasional epiphylls experience a lower pressure to establish rapidly on the surface of leaves, as they can normally colonize other substrates.

Alternatively, occasional epiphylls, which are primarily epiphytes, may rely more heavily on modes of dispersal other than asexual propagules. Devos et al. (2011) found no phylogenetic correlation between the production of asexual propagules and obligate epiphytes of the genus *Radula*. The authors suggest that the dispersal by whole gametophyte fragments is possibly the most efficient strategy for epiphytic liverworts because the fragments are shown to have a greater establishment rate than gemmae or spores (Löbel et al., 2009). It is possible that the epiphytes experience a more extreme environment than epiphylls and would therefore benefit more from dispersing by fragments rather than asexual propagules. Being primarily epiphytes, occasional epiphylls may still preferentially disperse by means of the whole gametophyte fragments. Thus, the selective advantage of having asexual propagules may have been reduced in these occasional epiphylls.

There was no evidence of correlated evolution between epiphyllly and the rest of the traits investigated in this study. For the five characters that were correlated with epiphyllly in the cross-species analysis, the analyses did not provide support for the correlation with epiphyllly in phylogenetic-based analyses (**Tables 1.2, 1.4**). These contradictory results suggest that the correlations observed in the cross-species analyses are a consequence of shared evolutionary history among closely related taxa, rather than independent evolution of these traits in response to epiphyllly (Felsenstein, 1985). For instance, epiphyllly was highly correlated with stem size and neotenic features in the cross-species analyses (**Table 1.2**), but the majority of these epiphyllous taxa with smaller stems and neotenic features were closely related members of the highly derived lineages within the *Tuyamaella-Cololejeunea* clade, as classified in Wilson et al. (2007a) and Gradstein et al. (2003). It is possible that this shared character of small stems allows many members of the *Tuyamaella-Cololejeunea* clade (such as *Cololejeunea* and *Colura*) to colonize the leaf surface, making the trait an “exaptation” in the sense of Gould and Vrba (1982).

The choice of traits might have contributed to the lack of correlations between epiphyllly and the selected traits in this study for two reasons. First, many of the proposed “adaptive” traits for epiphyllly are also hypothesized to be adaptations for tropical epiphytic liverworts. Water retention and quick establishment are common challenges for both leaf- and bark-dwelling liverworts in the tropics (Pócs, 1982). Traits such as inflated lobules and frequent asexual reproduction are also considered “adaptive” for bark species (Thiers, 1988b). Almost all liverworts in Lejeuneaceae are epiphytic (Gradstein et al., 2001), and several traits in the present study seem to be ancestral in the family (Wilson et al., 2007a). Therefore, it is possible that most

of the studied traits have evolved in response to epiphytism rather than epiphytally specifically (Devos et al., 2011).

The second reason has to do with whether these morphological characters are actually “adaptations” to epiphytally in the strict sense. Biologists often speculate about the adaptive functions of unique morphological characters without determining whether such “adaptations” have a causal relationship with the environment to which organisms adapt (Gould and Lewontin, 1979). Although the traits examined in this study might be important for survival on leaf surfaces now, they may have evolved for a different reason altogether.

The present study used the phylogenetic-based comparative analyses to distinguish production of asexual propagules from other traits as a key adaptive response to living on the leaf surface. The results provided additional support for the role of asexual propagules in the evolution of bryophytes in dynamic environments, as observed in previous ecological and comparative analyses (Devos et al., 2011; Zartman and Nascimento, 2006). Moreover, no other putative “adaptive” traits to epiphytally showed evidence of being a specific adaptation to epiphytally. The results of this study highlight the importance of phylogenetically controlled methods in determining an adaptive function of traits. Our ability to understand trait evolution in response to environment is central to answering other questions about diversification and extinction of plants, such as epiphytally, that depend on constantly changing habitats.

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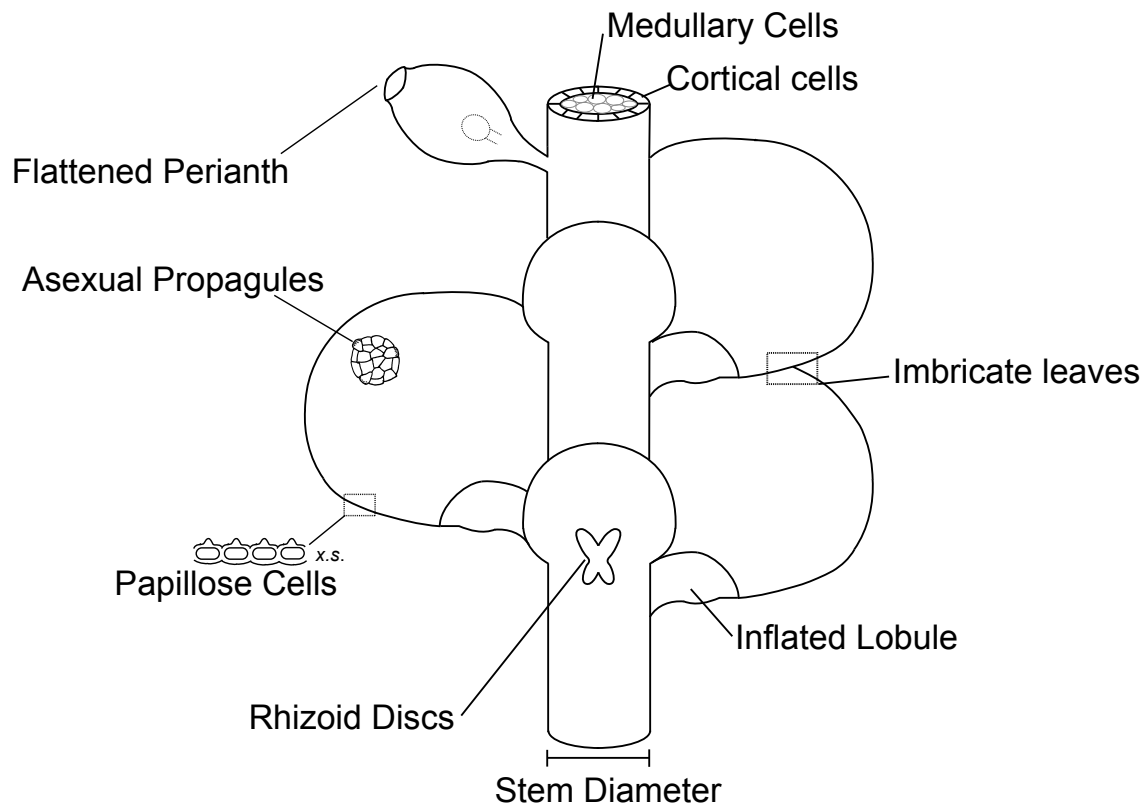


Figure 1.1: Schematic diagram illustrating some of the hypothesized “adaptive” traits of epiphyllous liverworts. Stem diameter, number of cortical, and medullary cells are summarized into a single trait, called stem size, using the first principal component of a principal component analysis (PCA). Stem size was hypothesized to be smaller in epiphyllous taxa. *Abbreviation: x.s.*, cross-section image.

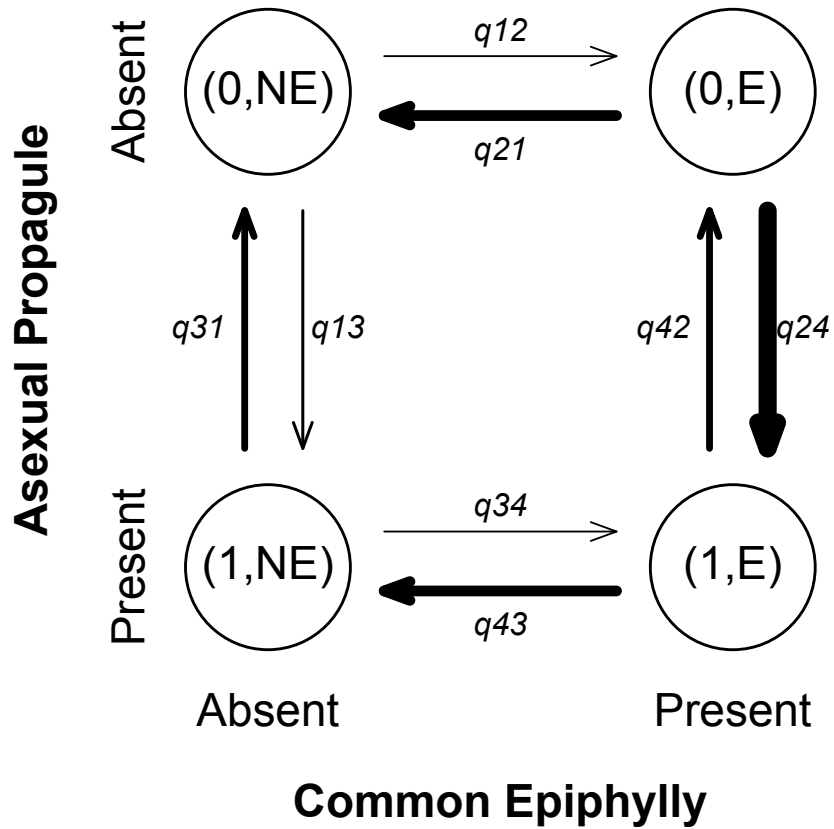


Figure 1.2: Schematic diagram illustrating transition rates of character states of asexual propagules in association with common epiphyllous. Stages: NE, non-epiphyllous; E, epiphyllous; asexual propagules: 0, absent; 1, present. Thickness of each arrow is scaled to the respective transition rate. Asexual propagule is more likely to evolve in an epiphyllous taxon ($q_{24} > q_{13}$; BF = 15.8).

Table 1.1. Taxa included in analyses and their associated trait data. Nomenclature follows Wilson et al. (2007a). The source of trait data is given after each taxon. Details on traits scoring are in the text. Abbreviations: Stem = small stem size, Sex = sexuality, Imb = imbricate leaves, Pap = papillose cells, Lob = inflated lobules, Per = flattened perianth, Asex = presence of asexual propagules, Neot = presence of neotenic feature, OccE = occasional epiphyll, ComE = common epiphyll. A question mark (?) indicates missing datum.

Taxon	Reference	Stem	Sex	Imb	Pap	Lob	Per	Asex	Neot	OccF	ComE	Note
<i>Acantbocoleus aberrans</i> (Lindenb. & Gottsche) Kruijt	Gradstein, 1994	0	1	1	0	1	0	0	0	0	0	
<i>Acantbocoleus javanicus</i> (Steph.) Kruijt	Kruijt, 1988	1	1	0	0	0	1	0	0	1	0	
<i>Acantbocoleus madagascariensis</i> (Steph.) Kruijt	Kruijt, 1988	1	1	1	0	1	1	0	0	0	0	
<i>Acrolejeunea fertilis</i> (Reinw. et al.) Schiffn. I	Gradstein, 1975	1	1	1	0	0	0	0	0	0	0	
<i>Acrolejeunea fertilis</i> II	Gradstein, 1975	1	1	1	0	0	0	0	0	0	0	
<i>Acrolejeunea parvula</i> (Mizut.) Gradst.	Gradstein, 1975	1	0	1	1	1	0	0	0	0	0	
<i>Acrolejeunea recurvata</i> Gradst.	Gradstein, 1975	0	0	1	0	0	1	1	0	0	0	
<i>Anoplojeunea conferta</i> (C.F.W. Meissn. ex Spreng.) A.Evans	Evans, 1908	?	0	1	0	1	0	0	0	0	0	
<i>Aphanolejeunea</i> sp.	Gradstein et al., 2001	1	1	0	1	1	0	1	1	1	1	Genus description used
<i>Archilejeunea fuscescens</i> (Hampe ex Lehm.) Fulf.	Gradstein, 1994	?	0	1	0	0	0	1	0	0	0	
<i>Archilejeunea ludoviciana</i> ssp. <i>porelloides</i> (Spruce) Gradst. & P.Geissler	Gradstein, 1994	?	0	1	0	0	0	1	0	0	0	
<i>Archilejeunea parviflora</i> (Nees) Schiffn.	Gradstein, 1994	?	1	1	0	0	0	1	0	0	0	
<i>Archilejeunea planiuscula</i> (Mitt.) Steph.	Gradstein et al., 2002	?	1	1	0	0	0	1	0	0	0	
<i>Aureolejeunea aurifera</i> R.M.Schust.	Schuster, 1987	1	1	1	1	1	0	0	0	0	0	
<i>Aureolejeunea fulva</i> R.M.Schust.	Schuster, 1987	0	1	1	0	1	0	0	0	0	0	
<i>Aureolejeunea quinquecarinata</i> R.M.Schust.	Schuster, 1987	?	1	1	0	1	0	0	0	0	0	
<i>Blepharolejeunea incongrua</i> (Lindenb.&Gott.) van Slageren & Kruijt	Gradstein, 1994	1	1	1	0	0	0	0	0	0	0	
<i>Brachiolejeunea laxifolia</i> (Tayl.) Schiffn.	Gradstein, 1994	0	1	1	0	1	0	0	0	1	0	
<i>Bryopteris diffusa</i> (Sw.) Nees	Gradstein, 1994	0	0	0	0	1	?	1	0	0	0	
<i>Bryopteris filicina</i> (Sw.) Nees	Gradstein, 1994	0	1	1	0	1	0	1	0	0	0	
<i>Caudalejeunea recurvistipula</i> (Gottsche) Schiffn.	Gradstein et al., 2002	?	1	0	0	0	0	1	0	0	0	
<i>Ceratolejeunea</i> cf. <i>guyanensis</i> (Nees & Mont.) Steph.	Dauphin, 2000	1	1	1	0	1	0	0	0	1	0	
<i>Ceratolejeunea cornuta</i> (Lindenb.) Steph.	Dauphin, 2000	?	1	0	0	1	0	?	0	1	0	
<i>Ceratolejeunea diversicornuta</i> Steph.	Vanden-Berghen, 1951	1	0	1	1	1	0	0	0	1	0	
<i>Ceratolejeunea grandiloba</i> J.B. Jack & Steph.	Dauphin, 2000	1	1	1	0	1	?	0	0	0	0	
<i>Cheilolejeunea acutangula</i> (Nees) Grolle	Spruce, 1884; Grolle, 1979	?	0	1	1	1	1	?	0	0	0	
<i>Cheilolejeunea clausa</i> (Nees & Mont.) R.M.Schust.	Schuster, 1980	1	0	1	0	1	0	0	0	0	0	

Taxon	Reference	Stem	Sex	Imb	Pap	Lob	Per	Asex	Neot	OccF	ComE	Note
<i>Cheilolejeunea lineata</i> A.Evans	Evans, 1906	?	0	1	0	1	1	?	0	0	0	As <i>Cystolejeunea lineata</i> (Lehm. & Lindenb.) Evans
<i>Cheilolejeunea meyeniana</i> (Gottsche, Lindenb. & Nees) R.M.Schust. & Kachroo	Stephani, 1914	?	0	0	0	1	0	?	0	1	0	As <i>Pycnolejeunea meyeniana</i> (Gottsche, Lindenb. & Nees) Steph.
<i>Cheilolejeunea revoluta</i> (Herz.) Gradst. & Grolle	Gradstein et al., 1993	0	0	1	1	1	0	0	0	0	0	
<i>Cheilolejeunea rigidula</i> (Mont.) R.M.Schust.	Schuster, 1980	1	0	1	0	1	1	?	0	0	0	
<i>Cheilolejeunea</i> sp. indet.	Gradstein et al., 2001	?	?	?	?	1	0	0	0	0	0	Genus description used
<i>Cheilolejeunea trifaria</i> (Reinw. et al.) Mizut.	Zhu and So, 2001	1	1	1	1	1	0	0	0	1	0	
<i>Cololejeunea laevigata</i> (Mitt.) Tilden	Thiers, 1988a	1	1	1	0	0	0	1	1	1	1	
<i>Cololejeunea metzgeriopsis</i> (K.I.Goebel) Gradst. et. al.	Gradstein et al., 2006	?	0	0	1	?	1	1	1	1	1	
<i>Cololejeunea obliqua</i> (Nees & Mont.) Schiffn.	Zhu et al., 1999	1	1	1	1	1	0	0	1	1	1	
<i>Cololejeunea peculiaris</i> (Herz.) Benedix	Thiers, 1988a	1	1	1	0	1	0	1	1	0	0	
<i>Cololejeunea vitalana</i> Tixier	Tixier, 1991	1	1	0	0	1	1	?	1	1	1	
<i>Cololejeunea vuquangensis</i> Pócs	Pócs and Ninh, 2005	1	1	1	0	0	0	0	1	0	0	
<i>Colura acroloba</i> (Mont. ex. Steph.) Ast	Zhu and So, 2001	1	1	1	0	1	0	1	1	1	1	
<i>Colura imperfecta</i> Steph.	Jovet-Ast, 1953	?	1	0	0	0	0	?	1	1	0	
<i>Colura tortifolia</i> (Mont. & Nees) Trevis.	Jovet-Ast, 1953	?	0	0	0	1	0	?	1	1	0	
<i>Cycololejeunea peruviana</i> (Lehm. & Lindenb.) A.Evans	Bernecker-Lücking, 1998	1	0	1	0	1	?	1	0	1	1	
<i>Dendrolejeunea fruticosa</i> (Lindenb. & Gottsche) Lacout.	Gradstein et al., 2002	?	0	1	0	0	0	?	0	0	0	
<i>Dicranolejeunea axillaris</i> (Nees & Mont.) Schiffn.	Gradstein, 1994	1	1	1	0	1	1	0	0	0	0	
<i>Diplasiolejeunea cavifolia</i> Steph.	Zhu and So, 2001	1	1	1	0	1	0	1	1	1	0	
<i>Diplasiolejeunea involuta</i> ssp. <i>andicola</i> Pócs.	Winkler, 1967; León et al., 1998	1	?	1	0	1	?	?	1	1	1	
<i>Diplasiolejeunea</i> sp.	Gradstein et al., 2001	1	?	1	0	1	0	1	1	1	1	Genus description used
<i>Drepanolejeunea anoplantba</i> (Spruce) Steph.	Bischler, 1964	1	0	0	1	1	0	1	0	0	0	
<i>Drepanolejeunea biocellata</i> A.Evans	Bischler, 1964	1	0	0	0	1	0	1	0	1	1	
<i>Drepanolejeunea</i> sp.	Gradstein et al., 2001	1	?	0	1	1	0	1	0	1	1	Genus description used
<i>Drepanolejeunea vesiculosa</i> (Mitt.) Steph.	Zhu and So, 2001	1	0	0	1	1	?	1	0	1	0	
<i>Evansiolejeunea roccatii</i> Vanden Berghen	Vanden-Berghen, 1948; Schuster, 2006	0	0	1	0	0	0	?	0	0	0	

Taxon	Reference	Stem	Sex	Imb	Pap	Lob	Per	Asex	Neot	OccF	ComE	Note
<i>Frullanoides corticalis</i> (Lehm. & Lindenb.) van Slageren	Gradstein, 1994	0	0	1	0	0	0	0	0	0	0	
<i>Frullanoides mexicana</i> van Slageren	Gradstein, 1994	0	0	1	0	0	0	0	0	0	0	
<i>Fulfordianthus evansii</i> (Fulford) Gradst.	Gradstein, 1994	0	0	1	0	1	0	0	0	0	0	
<i>Fulfordianthus pterobryoides</i> (Spruce) Gradst. I	Gradstein, 1994	0	0	1	0	1	0	0	0	0	0	
<i>Fulfordianthus pterobryoides</i> II	Gradstein, 1994	0	0	1	0	1	0	0	0	0	0	
<i>Harpalejeunea grandistipula</i> R.M.Schust.	Schuster, 1999	1	?	0	1	1	?	1	0	0	0	
<i>Jubula bogotensis</i> Steph.	Guerke, 1978	?	1	1	0	1	0	1	0	0	0	
<i>Jubula hutchinsiae</i> (Hook.) Dumort.	Guerke, 1978	?	1	0	0	1	0	1	0	0	0	
<i>Lejeunea cancellata</i> Nees & Mont. ex Mont.	Schuster, 1980	?	0	0	0	0	?	1	0	0	0	As <i>L. cardiophora</i> (Schust.) Schust.
<i>Lejeunea catinulifera</i> Spruce I	Reiner-Drehwald, 2005	1	0	1	0	1	0	1	0	0	0	
<i>Lejeunea catinulifera</i> II	Reiner-Drehwald, 2005	1	0	1	0	1	0	1	0	0	0	
<i>Lejeunea cavifolia</i> (Ehrh.) Lindb.	Schuster, 1980	1	0	1	0	1	0	?	0	0	0	
<i>Lejeunea cerina</i> (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees	Stephani, 1914	?	0	0	0	0	0	?	0	0	0	As <i>Hygrolejeunea cerina</i> (Lehm. & Lindenb.) Steph
<i>Lejeunea eckloniana</i> Lindenb.	Jones, 1974	1	1	1	0	1	0	0	0	0	0	
<i>Lejeunea exilis</i> (Reinw. et al.) Grolle	Zhu and Grolle, 2003	1	0	0	0	1	1	1	0	1	0	
<i>Lejeunea flava</i> (Sw.) Nees I	Schuster, 1980	1	1	1	0	1	0	?	0	1	0	
<i>Lejeunea flava</i> II	Schuster, 1980	1	1	1	0	1	0	?	0	1	0	
<i>Lejeunea laetevirens</i> Nees & Mont.	Schuster, 1980	1	0	0	0	1	0	0	0	0	0	
<i>Lejeunea lamacerina</i> (Steph.) Schiffn.	Schuster, 1980	?	1	1	0	1	0	0	0	0	0	As <i>L. lamacerina</i> subsp. <i>gemminata</i> Schust.
<i>Lejeunea mimula</i> Hürl.	Mizutani, 1970	0	?	1	?	?	0	?	0	0	0	As <i>L. luteola</i> (Steph.) Mizt.
<i>Lejeunea pallescens</i> Mitt.	Mitten, 1851; Spruce, 1884	?	0	0	0	1	0	?	0	0	0	
<i>Lejeunea paucidentata</i> (Steph.) Grolle	Stephani, 1896; Grolle, 1991	?	1	0	0	1	0	?	0	0	0	As <i>Crossotolejeunea paucidentata</i> Steph.
<i>Lepidolejeunea eluta</i> (Nees) R.M.Schust. I	Piippo, 1986	0	0	1	0	0	0	0	0	0	0	
<i>Lepidolejeunea eluta</i> II	Piippo, 1986	0	0	1	0	0	0	0	0	0	0	
<i>Lepidolejeunea integrastipula</i> (Jack & Steph.) R.M.Schust.	Piippo, 1986	1	0	1	0	1	0	1	0	0	0	
<i>Leptolejeunea elliptica</i> (Lehm. & Lindenb.) Schiffn.	Zhu and So, 2001	1	1	0	0	1	0	1	0	1	1	
<i>Leucolejeunea chypeata</i> (Schwein.) A.Evans	Schuster, 1980	1	1	1	0	1	0	0	0	0	0	
<i>Leucolejeunea xanthocarpa</i> (Lehm. & Lindenb.) A.Evans I	Schuster, 1980	1	1	1	0	1	1	0	0	0	0	
<i>Leucolejeunea xanthocarpa</i> II	Schuster, 1980	1	1	1	0	1	1	0	0	0	0	

Taxon	Reference	Stem	Sex	Imb	Pap	Lob	Per	Asex	Neot	OccF	ComE	Note
<i>Lindigianthus cipaconeus</i> (Gottsche) Kruijt & Gradst.	Gradstein, 1994	0	0	1	0	1	1	0	0	1	0	
<i>Lopholejeunea ceylanica</i> Steph.	Zhu and Gradstein, 2005	1	0	1	0	1	1	0	0	0	0	
<i>Lopholejeunea enlopha</i> (Tayl.) Schiffn. I	Zhu and Gradstein, 2005	1	0	1	0	1	0	1	0	1	0	
<i>Lopholejeunea enlopha</i> II	Zhu and Gradstein, 2005	1	0	1	0	1	0	1	0	1	0	
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.	Zhu and Gradstein, 2005	1	1	1	0	1	0	0	0	1	0	
<i>Luteolejeunea herzogii</i> (Buchloh) Piippo	Piippo, 1986	1	0	1	0	1	0	0	0	0	0	
<i>Macrocolura sagittistipula</i> (Spruce) R.M.Schust.	Grolle and Zhu, 2002	1	1	1	0	1	0	1	0	1	0	
<i>Marchesinia brachiata</i> (Sw.) Schiffn. I	Gradstein, 1994	?	0	1	0	0	1	1	0	0	0	
<i>Marchesinia brachiata</i> II	Gradstein, 1994	?	0	1	0	0	1	1	0	0	0	
<i>Marchesinia brachiata</i> III	Gradstein, 1994	?	0	1	0	0	1	1	0	0	0	
<i>Marchesinia robusta</i> (Mitt.) Schiffn.	Gradstein, 1994	?	0	1	0	0	1	1	0	0	0	
<i>Mastigolejeunea auriculata</i> (Wilson & W.J.Hooker) Schiffn. I	Gradstein, 1994	0	0	1	0	1	1	1	0	0	0	
<i>Mastigolejeunea auriculata</i> II	Gradstein, 1994	0	0	1	0	1	1	1	0	0	0	
<i>Mastigolejeunea ligulata</i> (Lehm. & Lindenb.)	Gradstein et al., 2002	1	1	1	0	1	0	?	0	0	0	
<i>Myriocolea irrorata</i> Spruce	Gradstein et al. 2001	1	1	0	0	0	1	1	1	0	0	
<i>Myriocoleopsis gymnocolea</i> (Steph.) E.Reiner & Gradst.	Reiner-Drehwald and Gradstein, 1995	?	1	0	0	0	0	0	1	0	0	
<i>Neopotamolejeunea</i> sp. nov.	Reiner-Drehwald, 2000	1	1	0	0	0	0	0	0	1	0	Genus description used
<i>Neurolejeunea brentelii</i> (Gottsche) A.Evans I	Gradstein, 1994	1	0	1	1	1	0	0	0	0	0	
<i>Neurolejeunea brentelii</i> II	Gradstein, 1994	1	0	1	1	1	0	0	0	0	0	
<i>Nipponolejeunea subalpina</i> (Horik.) S.Hatt.	Bakalin et al., 2005	1	0	1	0	1	0	0	0	0	0	
<i>Odontolejeunea lunulata</i> (F.Weber) Schiffn.	Gradstein, 1994	1	0	1	0	1	1	1	0	1	1	
<i>Omphalanthus filiformis</i> (Sw.) Nees I	Evans, 1907	?	0	1	0	1	0	0	0	0	0	
<i>Omphalanthus filiformis</i> II	Evans, 1907	?	0	1	0	1	0	0	0	0	0	
<i>Omphalanthus ovalis</i> (Lindenb. & Gottsche) Gradst.	Gradstein et al., 2001; Schuster, 2006	?	0	1	0	0	0	0	0	0	0	
<i>Phaeolejeunea amicornum</i> (Hürlimann) Pócs	Pócs, 2008	0	?	1	1	0	?	?	0	0	0	
<i>Physantholejeunea portoricensis</i> (Hampe&Gott.) Schust.	Evans, 1907; Gradstein, Churchill, and Salazar-Allen, 2001	?	0	1	0	1	0	0	0	0	0	
<i>Pluvianthus squarrosus</i> (Steph.)	Schuster and Schäfer-Verwimp, 1995	1	1	1	0	1	0	0	0	0	0	
<i>Ptychanthus striatus</i> (Lehm. & Lindenb.) Nees I	Gradstein et al., 2002	0	1	1	0	0	0	?	0	0	0	
<i>Ptychanthus striatus</i> II	Gradstein et al., 2002	0	1	1	0	0	0	?	0	0	0	
<i>Ptychanthus striatus</i> III	Gradstein et al., 2002	0	1	1	0	0	0	?	0	0	0	
<i>Pycnolejeunea densistipula</i> (Lehm. & Lindenb.) Nees	He, 1999	0	1	1	0	1	0	1	0	0	0	
<i>Rectolejeunea berteriana</i> (Gottsche) A.Evans	He, 1997	1	0	1	0	1	?	1	0	1	0	

Taxon	Reference	Stem	Sex	Imb	Pap	Lob	Per	Asex	Neot	OccF	ComE	Note
<i>Schiffneriolejeunea nymannii</i> (Steph.) Gradst. & Terken	Gradstein and Terken, 1981	0	0	1	0	1	0	1	0	0	0	
<i>Schiffneriolejeunea pappeana</i> (Nees) Gradst.	Gradstein and Vanden-Berghen, 1985	0	0	1	0	1	0	?	0	1	0	
<i>Schiffneriolejeunea tumida</i> (Nees & Mont.) Gradst. var. <i>baskarliana</i> (Gottsche) Gradst. & Terken	Gradstein and Terken, 1981	0	0	1	0	1	0	1	0	0	0	
<i>Siphonolejeunea elegantissima</i> (Steph.) Grolle	Grolle, 1976	?	1	0	1	1	0	0	0	1	1	
<i>Spruceanthus theobromae</i> (Spruce) Gradst.	Gradstein, 1994	0	1	1	0	0	0	0	0	0	0	
<i>Spruceanthus thozetianus</i> (Gottsche & F.v.Müll) B.Thiers	Thiers and Gradstein, 1989	?	0	1	0	1	1	?	0	0	0	
<i>Stictolejeunea squamata</i> (Willd. ex Web.) Schiffn.	Gradstein, 1994	0	0	1	0	1	0	0	0	1	0	
<i>Symbiezidium barbiflorum</i> (Gott.) A.Evans	Gradstein, 1994	0	1	1	0	1	1	0	0	1	0	
<i>Symbiezidium dentatum</i> Herz.	Gradstein, 1994	0	1	1	0	1	1	0	0	1	0	
<i>Symbiezidium transversale</i> (Sw.) Trevis. var. <i>transversale</i>	Gradstein, 1994	0	1	1	0	1	1	0	0	1	0	
<i>Taxilejeunea</i> cf. <i>asthenica</i> (Spruce) Steph.	Spruce, 1884	?	1	1	0	0	0	?	0	0	0	
<i>Taxilejeunea</i> cf. <i>isocalycina</i> (Nees) Steph.	Stephani, 1913	?	1	0	0	0	0	?	0	0	0	
<i>Taxilejeunea</i> cf. <i>pterigonia</i> (Lehm. & Lindenb.) Schiffn.	Evans, 1907	?	1	1	0	0	0	?	0	0	0	
<i>Taxilejeunea</i> sp.	Gradstein et al., 2001	?	1	1	0	0	0	0	0	1	0	Genus description used
<i>Thysananthus anguiformis</i> (Hook.f. & Taylor)	Hooker and Fitch, 1855; Gradstein et al., 2001	?	?	1	?	?	1	0	0	0	0	
<i>Thysananthus comosus</i> Lindenb. ex Lehm.	Fulford, 1941	?	0	1	0	1	1	0	0	0	0	
<i>Thysananthus convolutus</i> Lindenb. I	Gradstein et al., 2002	?	0	1	0	0	0	0	0	0	0	
<i>Thysananthus convolutus</i> II	Gradstein et al., 2002	?	0	1	0	0	0	0	0	0	0	
<i>Thysananthus spathulistipus</i> (Reinw. et al.) Lindenb.	Thiers and Gradstein, 1989	?	1	1	0	1	1	?	0	0	0	
<i>Xylolejeunea crenata</i> (Nees & Mont.) X.-L. He & Grolle	He and Grolle, 2001	1	1	1	0	1	0	1	0	0	0	

Table 1.2: Associated traits of selected leafy liverworts in Lejeuneaceae, their character states, and cross-species analyses of correlations between epiphylls and the traits. *P*-values are calculated from Pearson’s χ^2 test for proportion. Asterisks (*) indicate $P < 0.05$ without corrections for multiple comparisons.

Character	State	Number of taxa				<i>P</i> -value all epiphyll ^a	<i>P</i> -value common epiphyll
		All	Not epiphyll	Occasional epiphyll	Common epiphyll		
Sexuality	0 = dioicy	126	50	11	4	0.11	0.45
	1 = monoicy		38	16	7		
Leaf Position	0 = distant	133	13	8	7	0.006*	0.013*
	1 = imbricate		79	19	7		
Cell surface	0 = smooth	131	81	24	9	0.22	0.023*
	1 = papillose		9	3	5		
Lobule	0 = flattened	131	35	4	1	0.005*	0.12
	1 = inflated		56	23	12		
Perianth	0 = inflated	125	68	19	9	0.97	0.83
	1 = flattened		20	6	3		
Asexual propagules	0 = absent	105	45	13	2	0.23	0.007*
	1 = present		28	7	10		
Neotenic features	0 = absent	134	89	24	6	<0.001*	<0.001*
	1 = present		4	3	8		
Stem size	0 = large	91	25	7	0	0.04*	0.02*
	1 = small		32	15	12		

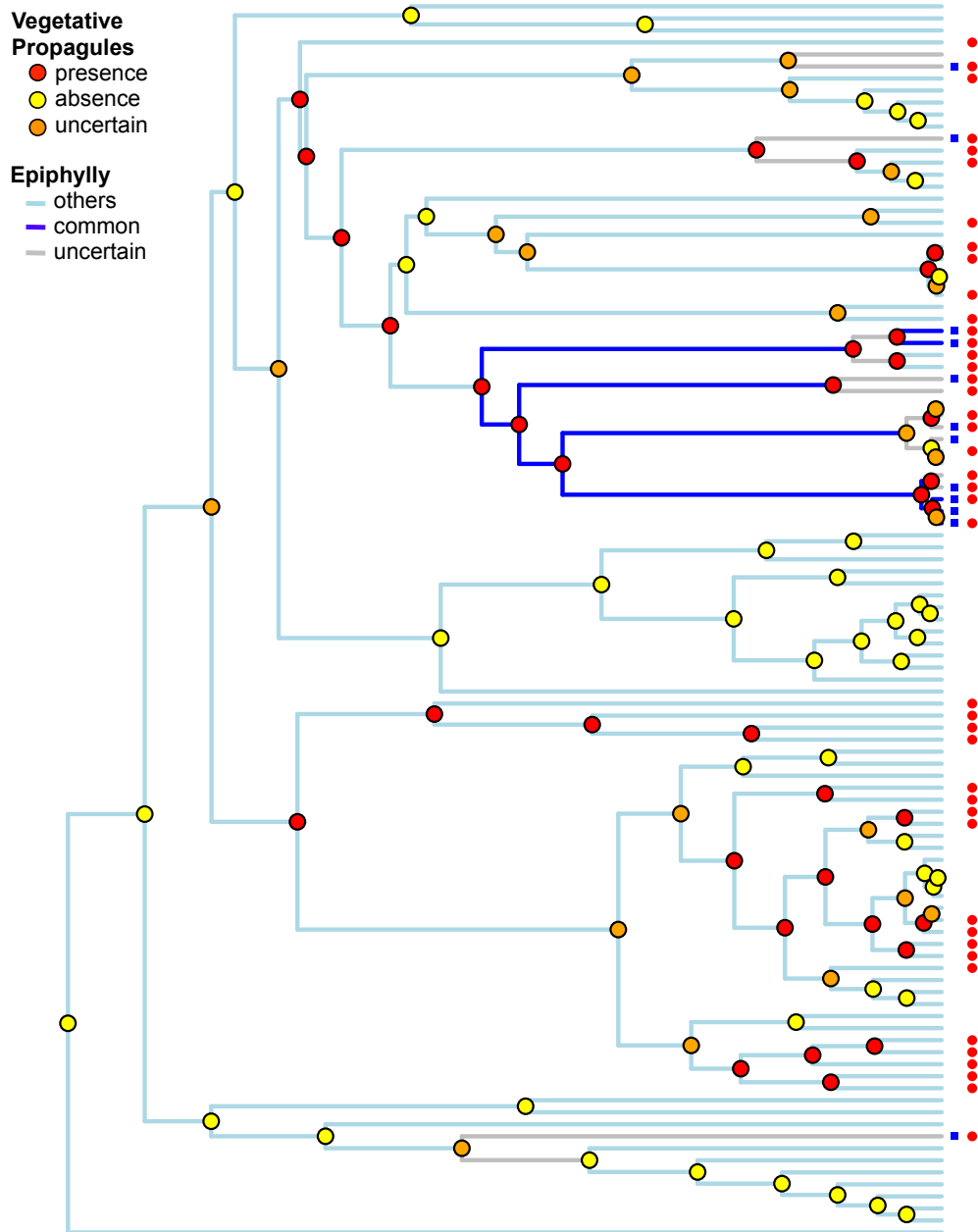
^a All epiphylls comprised of both occasional and common epiphyllous taxa.

Table 1.3: Comparisons of transition rate parameters between two competing models for Pagel’s correlated evolution analysis. (A) An independent model assumes that the transition rate between character states of one character does not depend on the other trait’s state; (B) a dependent model assumes otherwise (Pagel, 1994). The character state before a comma refers to the presence (1) and absence (0) of the studied traits. The character state after the comma refers to the presence (E) and absence (0) of epiphylls. The simultaneous transitions for both traits are set to zero. Ellipses (...) represent the values of main diagonal elements, which are set to be the minus of the sum of each row, so that the sum of elements in the row is zero.

From/to	0,0	0,E	1,0	1,E
A) Independent model (4 parameters)				
0,0	...	a_1	b_1	0
0,E	a_2	...	0	b_2
1,0	b_1	0	...	a_1
1,E	0	b_2	a_2	...
B) Dependent model (8 parameters)				
0,0	...	q_{12}	q_{13}	0
0,E	q_{21}	...	0	q_{24}
1,0	q_{31}	0	...	q_{34}
1,E	0	q_{42}	q_{43}	...

Table 1.4: Harmonic means of log-likelihoods of the two competing models, independent [L(I)] and dependent [L(D)] models in Pagel’s correlated evolution analysis of traits in the leafy liverworts family Lejeuneaceae. A positive-associated Bayes factor (BF) greater than 3 provides a strong support for the dependent model. The best-fitting model in each analysis is in boldface.

Trait	Correlation with all epiphyll			Correlation with common epiphyll		
	L(I)	L(D)	BF	L(I)	L(D)	BF
Sexuality	-166.95	-161.96	-9.99	-128.68	-122.81	-11.73
Leaf position	-143.28	-143.98	1.39	-106.29	-104.01	-4.56
Cell surface	-130.55	-127.43	-6.25	-90.16	-87.60	-5.13
Lobule	-153.08	-151.54	-3.07	-116.58	-114.98	-3.20
Perianth	-152.21	-145.22	-13.98	-109.91	-106.63	-6.56
Asexual propagules	-148.60	-136.96	-23.27	-97.64	-99.18	3.08
Neotenic feature	-94.62	-94.31	0.62	-52.81	-53.11	-0.60
Stem size	-136.05	-126.71	-18.68	-92.89	-87.90	-9.98



Appendix 1.1: Ancestral state reconstruction of the production of vegetative (asexual) propagules and “common epiphyllous” in leafy liverworts (*Lejeuneaceae*), using a maximum likelihood method. Each branch color indicates the reconstructed state of “common epiphyllous” (see legends). Each node color indicates the reconstructed state (presence/absence) or asexual propagules. At the tips, a blue square indicates a taxon with “common epiphyllous”, and a red circle indicates a taxon that produces asexual propagules.

CHAPTER 2:

Microclimate Fluctuation Correlated with Beta Diversity of Epiphyllous Bryophyte Communities

ABSTRACT

Site-to-site variation in community composition, or beta diversity, is a major component of regional diversity. However, we have little understanding of factors that regulate beta diversity. The current study uses leaf-colonizing (epiphyllous) bryophyte communities as a model system to investigate the effects of microclimate on beta diversity. A total of 354 epiphyllous bryophyte communities from 18 sites on the island of Moorea, French Polynesia were collected and identified. At each site, temperature and relative humidity were measured and converted to vapor pressure deficit (VPD). The analysis showed that beta diversity among communities on different host types increased with the increasing daily range of VPD at a given site. It is possible that high fluctuation in microclimate conditions augments the differences in habitat quality among host types, resulting in greater dissimilarities among epiphyllous communities. However, host niche breadths of major epiphyllous species do not decrease with increasing VPD range, suggesting the observed pattern may be the results of other mechanisms than reduction in host niche breadths.

Keywords: Epiphylls, Bryophytes, Community, Beta Diversity, Microclimate, Vapor Pressure Deficits

INTRODUCTION

Beta diversity, defined as compositional variation among local communities, has garnered increasing interest in recent years, as many ecologists move their focus to describing and understanding large-scale patterns of biodiversity (Anderson et al., 2011). This renewed interest has led to a proliferation of studies establishing various patterns of beta diversity across gradients (Keil et al., 2012; Tang et al., 2013). However, many of these studies rely on previously collected datasets that were not specifically designed to study patterns of beta diversity, making them subject to criticism (Kraft et al., 2011; Qian et al., 2012; Tuomisto and Ruokolainen, 2012). It is only recently that data were collected specifically to demonstrate patterns and infer the mechanisms behind observed patterns of beta diversity (Harrison et al., 2006; Myers et al., 2013; Fernandez Goñi, 2013).

High levels of beta diversity are often attributed to habitat heterogeneity and habitat selection (Whittaker, 1972). It is assumed that differences in patch qualities lead to non-random colonization of organisms (Davies et al., 2005). Studies of Californian plants, for example, show a high level of beta diversity between serpentine and non-serpentine habitats, suggesting a strong role of habitat qualities in producing beta diversity (Harrison et al., 2006; Anacker and Harrison, 2012). However, Myers et al. (2013) have shown that high beta diversity can also be the result of dispersal limitation. However, these types of study in plants often require a large sample size across a large geographical scale to infer patterns and processes.

Discrete in both space and time, small communities of leaf-colonizing (epiphyllous) bryophytes provide an excellent system for the study of beta diversity. A large number of

epiphyllous communities can be obtained from a small area and extended across multiple habitat types and scales. They occur ubiquitously in most of the humid tropical forests and can be preserved intact for later examination (Richards, 1932). Despite these advantages, the system has not been used for a study of patterns and processes of beta diversity.

As a host for bryophytes, leaves of vascular plants differ dramatically in their physical and chemical properties (Müller and Riederer, 2005). Such variations result in functional differences among leaves and have been shown to affect the colonization of epiphyllous bryophytes (Brenes-Arguedas et al., 2006; Andreas, 2011). Various natural history accounts reported some associations of epiphyllous bryophytes with their host leaves (Lücking, 1995; Pócs, 1996). However, previous studies on epiphylls have not quantitatively confirmed this prediction of compositional variation, or beta diversity, among leaves (Winkler, 1967; Coley et al., 1993).

One possible reason why host association of epiphyllous bryophytes remains unclear may have to do with microclimatic factors. A recent study from Costa Rica demonstrated the correlations between community structures and microclimates (Sonnleitner et al., 2009). Most previous analyses of host specificity include community data on hosts from a wide range of different microclimates, and therefore, are unable to separate the effects of host characters from the microclimates. Microtopographical differences of the leaf surface among hosts may be exaggerated by microclimatic factors, resulting in variation in the degree of host specificity. The boundary layer on a leaf surface provides a dramatically different condition from the ambient environment for epiphyllous organisms (Morris, 2002). Therefore, a slight difference in microclimatic conditions may lead to a greater difference among leaves in habitat qualities for bryophytes. Olaninmoye (1975) particularly suggested that host specificity might be stronger in a “less favorable” environment. In the other words, the use of available hosts by a bryophyte taxon (its “niche breadth”; Feinsinger et al., 1981) may be reduced in a more stressful environment. In tropical bryophytes, high variation in the water environment is a likely source of stress, as these bryophytes are usually not known to be desiccation tolerant (Zhu and So, 2001). However, a spatially explicit sampling with microclimate data is required to test this hypothesis.

The current study examined epiphyllous bryophyte community to quantify the effect of microclimate fluctuation on beta diversity among host types. Specifically I asked the following questions: 1) Does beta diversity change along a gradient of microclimate fluctuation? 2) Is change in beta diversity associated with reduction in host niche breadths of epiphyllous species? I hypothesized that beta diversity would increase with increasing fluctuation of habitat microclimate, as measured by the daily range of vapor pressure deficit (VPD). The increase of beta diversity was also expected to be associated with the reduction in host niche breadth of epiphyllous taxa.

METHODS

Study Area - The study was conducted on the island of Moorea (17° 29' 25" S, 149°49' 34" W). As part of the Society Islands, French Polynesia, Moorea lies roughly 17 km northwest of Tahiti with an area of 134 square kilometers. The study area was limited to the mid-elevation secondary forest (118-241 m above sea level) in the Opunohu Valley, where the majority of land is preserved from cultivation and tourism. Average annual precipitation of this area is 325 cm (Resh et al., 1990). After 2,000 years of extensive land use by Polynesians, the area was mostly

abandoned since the European arrival in 1768 (Green et al., 1967; Lepofsky et al., 1996). The common canopy tree species include Tahitian Chestnut (*Inocarpus fagifer*), Sea Hibiscus (*Hibiscus tiliaceus*), Malay Apple (*Syzygium malaccense*), Candlenut (*Aleurite moluccana*), and Mara (*Neonauclia fosteri*). The understory layer is normally composed of seedlings and saplings of canopy trees, as well as *Eugenia reinwardtiana*, *Freycinetia* spp., *Spathoglottis plicata*, and various ferns (*Angiopteris evecta*, *Bolbitis lonchophora*, *Teraphyllum wilkesianum*, *Lomariopsis brachenridgei*, and *Nephrolepis hirsutula*).

Study plots were selected based on the availability of hosts and their daily ranges in Vapor Pressure Deficit (VPD). Each 3x3-m² contained three host types. Two combinations of host species were chosen, based on their abundance in the study area. Host combination 1 consisted of seedlings of two angiosperms (*I. fagifer* and *S. malaccense*) and a fern (*B. lonchophora*). Host combination 2 consisted of *I. fagifer* seedling and two ferns (*B. lonchophora* and *T. wilkesianum*). Due to patchy distributions of these hosts in the landscape, only eleven plots with host combination 1 and seven plots with host combination 2 were selected. For each host combination, the plots were at least six meters apart, but the overall area did not exceed one sq.km² in order to minimize effect of climatic differences at a larger scale. In each plot, one to three leaves were collected from at least one plant from each host species, resulting in a total of 354 leaves. The samples were pressed and dry-preserved for identification in the laboratory at University of California, Berkeley.

VPD has been used to quantify the water environment for bryophytes (Fenton and Bergeron, 2006; Sporn et al., 2009), because it captures the effects of both temperature and relative humidity on the water vapor available plants (Jones, 1992). For this study, air temperature and relative humidity were recorded every five minutes for five consecutive days during the dry season (September to October) of 2011, using data loggers (EL-USB2, Lascar Electronics, Erie, PA, USA). Due to the limitation of equipment, the measurements were taken for plots in one host combination at the time, and a calibration between the two sets of plot could not be made. The value of VPD for each plot was then calculated, using the formula from Jones (1992) and Tu (2010). The daily range of VPD is the average of the differences between the highest and the lowest VPDs in a 24-hour period.

Identification and community assessment - The epiphyllous bryophytes were identified under the dissecting and compound microscopes. Identification and nomenclatures in this study followed the conventions in Zhu and So (2001) and Lücking (1995). Vouchers were deposited in University of California (UC) Herbarium. Abundance of each taxon on the leaf was determined using the cover class system: 1 for 5%, 2 for 5-10%, 3 for 10-25%, 4 for 25-50%, and 5 for > 50%. This cover class method has been shown to be appropriate for other cryptogamic (bryophytes and lichens) community data (McCune and Grace, 2002). Leaf area and total cover by all taxa were determined from the scanned images of the leaves using the ImageJ software (Schneider et al., 2012).

Beta diversity - In order to calculate beta diversity among host types in each plot, the average abundance of each taxon on each host type was determined and subsequently used in the test for Multivariate homogeneity of group dispersions (PERMDISP2 procedures; betadisper function in R's vegan package; McArdle and Anderson, 2001). The mean distance of communities from the centroid of the plot was used as a measure for beta diversity, in the sense that it represents "variation" among communities (Anderson et al., 2006; Anderson et al., 2011). To determine whether beta diversity changed with increasing VPD range, a linear regression was performed on each of the host combinations. A linear mixed-effect model was also applied to

both combinations to assess the overall effect of VPD on beta diversity within each plot, using host combination as a random factor.

Null model - a null model was constructed by randomly sampling (without replacement) an abundance value of each bryophyte taxon from the observed dataset onto a leaf over 999 iterations. By maintaining the total biomass and species pool within a plot, this null model allowed us to test whether the observed beta diversity can be replicated by random colonization (Gotelli and Graves, 1996). The standardized difference from the null expectation, or beta deviation, was calculated by dividing the difference between the observed and expected values by the standard deviation of the expected values (Kraft et al., 2011; Myers et al., 2013). A value of beta deviation below zero indicates a lower value of beta diversity than expected from the null model, while a value above zero indicates a greater value of beta diversity than expected from the null model.

Host niche breadth - For each plot, niche breadth of five major epiphyllous species from each host combination was calculated to determine whether the pattern in beta diversity could be explained by the change in host utilization. These five species occurred in more than half of studied plots that spanned the studied gradient of VPD range. In host combination 1, the major bryophyte taxa were *Cololejeunea denticulata*, *C. lanciloba*, *Drepanolejeunea polyrhiza*, *Lejeunea* sp., and *Leptolejeunea epiphylla*. In host combination 2, the major taxa were almost identical to those in the host combination 1, except that *C. denticulata* was missing from this combination and replaced by *C. planissima*. The Proportional Similarity (PS) was used as a measure of host niche breadth (Feinsinger et al., 1981), as it was shown to perform better than the traditional Levins' index, which did not take the resource availability into account (Smith, 1982; Bolnick et al., 2002). In the case of epiphyllous bryophytes, the total surface area of each host is the total resource available, and the proportion of leaf surface covered by each species was the measure of resource use. A niche breadth value of 1 indicates a broad niche (non-specific use of resource), whereas a lower value indicates narrower niche, or more specific use of resource available. The relationship between niche breadth and VPD range was determined using a linear regression with alpha at 0.05.

All statistical analyses and data management were conducted in R statistical programming language (Version 2.15, R Core Team, 2012) with additional packages: *vegan* (Oksanen et al., 2012), *nlme* (Pinheiro et al., 2012), *plyr* (Wickham, 2011), *reshape2* (Wickham, 2007), and *picante* (Kembel et al., 2010).

RESULTS

Beta diversity - In host combination 1, beta diversity among host types increased significantly with increasing VPD range (linear regression, $r^2 = 0.39$, $P = 0.02$; **Fig. 2.1A**). In host combination 2, beta diversity also showed a slight increase with increasing VPD (linear regression, $r^2 = 0.23$, $P = 0.15$, **Fig. 2.1B**). With host combination as a random factor in the regression model, beta diversity increased significantly with increasing VPD range overall (linear mixed-effect model, $P = 0.01$).

When compared with beta diversity from the null model, the observed beta diversities in host combination 1 were lower than expected at the lower VPD range (Beta deviation < 0 , **Fig. 2.2A**) and deviated positively from the null values with increasing VPD range (Beta deviation > 0 , **Fig. 2.2A**). The patterns were not as clear in host combination 2 (**Fig. 2.2B**).

Host niche breadth - Among the five major bryophytes on host combination 1, the most abundant species in the system, *L. epiphylla*, consistently had a niche breadth close to 1 (**Fig. 2.3**). Niche breadth of *C. denticulata*, *D. polyrhiza* and *Lejeunea* sp. exhibited negative relationships with the VPD range (**Fig. 2.3**, slope estimates = -0.03 , -0.67 , -1.4 , respectively). *C. lanciloba* showed a slight increase in niche breadth with increasing VPD range. However, none of these relationships was statistically significant (linear regression, $P \geq 0.08$, $0 \leq r^2 \leq 0.46$)

For host combination 2, *L. epiphylla* similarly maintained a niche breadth close to 1. The niche breadth of *C. lanciloba* seemed to fluctuate narrowly around 0.75 and 1. The patterns of VPD range and niche breadth of other species did not appear to be linear, because r^2 values were low ($0 \leq r^2 \leq 0.20$, **Fig. 2.4**), and none of the linear regressions showed a significant difference of the slope estimate from zero (linear regression, $P \geq 0.43$).

DISCUSSION

The results support the hypothesis that beta diversity will increase with the increasing microclimate fluctuation (in this case, the daily VPD range). The deviation from the null model also demonstrated that random colonization could not reproduce the observed pattern of increasing beta diversity. In host combination 1, at a low VPD range, the observed beta diversity was lower than random colonization. The opposite held true at a higher VPD range, where the observed beta diversity exceeded the expectation from the null values. These patterns are consistent with the findings from previous studies that, although tropical epiphytes generally exhibit low host specificity (Pócs, 1982; Richards, 1984; Kürschner, 1990), their distribution on different hosts is not entirely random (Laube and Zotz, 2006).

Since host plants interact with epiphyllous species mostly at the leaf surface (Berrie and Eze, 1975; Müller and Riederer, 2005), the observed pattern of beta diversity can be attributed to interactive effects of host surface and microclimate on epiphyllous communities. Chemical properties of a leaf surface have been shown to affect the growth and communities of epiphyllous bryophytes (Andreas, 2011). While the leaf chemistry traits are fairly conserved within species (Asner and Martin, 2010), wettability and composition of wax compounds can change with microclimate variability (Koch et al., 2006). In epiphyllous fungi, these changes in leaf surface properties affect establishment of spores (Bradley et al., 2003). In the current study, the host types vary in their leaf surface properties, especially waxiness. *S. malaccense* appears to be the waxiest, while the ferns (*B. lonchophora* and *T. wilkesianum*) are the least waxy. Because waxy surfaces of tropical leaves function to repel water (Holder, 2007), epiphyllous bryophytes often do not establish well, or have a slow growth rate, on waxy leaves (Andreas, 2011). Therefore, it is possible that a high fluctuation in microclimate conditions augments the differences in the habitat quality among host types, resulting in greater dissimilarities among epiphyllous communities. Further detailed studies on leaf surface chemistry along microclimate gradients, as well as colonization experiments, are needed to test this hypothesis.

The increase in beta diversity with the VPD range is not strongly associated with reduction in niche breadth of epiphyllous species. In the host combination 1, only *Lejeunea* sp. exhibited a strong, although not statistically significant, reduction in niche breadth. The results partially support the hypothesis that epiphylls are more restricted in their colonization on hosts in “less favorable” localities, as defined by VPD range in this study (Olarinmoye, 1975). Whittaker

(1972) also proposed the idea of reduced niche breadth in fluctuating environments when discussing the relationship between diversity and “environmental favorableness.” However, this hypothesis has not been rigorously tested, due to the difficulty of quantifying niche axes and defining “favorableness” (Terborgh, 1973; Morin, 2011). In bryophytes, most studies on niche breadth were conducted in *Sphagnum*-dominated systems, where niche breadths were relatively low in undisturbed bogs, compared to disturbed sites (Soro et al., 1999). On the other hand, epixylic (rock-colonizing) liverworts showed relatively broad niches, suggesting that, in comparisons to other bryophytes, liverworts might be more of a generalist (Slack, 1997; Laaka-Lindberg et al., 2005). Another reason for little reduction in niche breadth might have to do with the measurement itself. In this study, the niche breadths were measured by the resource use at the adult stage, which might not reflect the actual reduction in host utilization along the microclimate gradients (Slack, 1997). Early establishment by asexual propagules or spores has been suggested to be a critical part of bryophyte community development (Rydin, 1986). A further study on niche breadth of propagules or juveniles might allow us to determine whether the observed increased beta diversity was in fact associated with the reduction of niche breadth.

Epiphyllous communities on host combination 2 exhibited similar, but less conclusive patterns of beta diversity and niche breadth along the VPD range gradient. While a similar set of mechanisms may be operating, two possible reasons may explain why the changes are not significant in this host combination. First, the hosts in the combination may be more similar to each other in their leaf surface chemistry than those in the combination 1, because two of the hosts in the combination 2 – *B. lonchophora* and *T. wilkesianum* – belong to the same family of ferns (Elaphoglossaceae) and are closely related (Schuettpelz and Pryer, 2007), as opposed to combination 1 that included three hosts from three entirely different orders. Leaf chemistry traits have been shown to be phylogenetically conserved (Asner and Martin, 2010). Therefore, the differences in leaf surface between these two ferns may have not been sufficient to produce a strong pattern of beta diversity. Second, this combination of hosts is distributed along a narrower span (0.37-0.48 kPa) of VPD range gradient than combination 1 (0.57 – 0.94 kPa). This narrow span of microclimate gradient might not provide sufficient statistical power to demonstrate a pattern of beta diversity.

In conclusion, this study demonstrates a pattern of beta diversity along a microclimate gradient, as well as the utility of epiphyllous bryophyte communities as a system to study beta diversity at a small scale. These results contribute to our growing knowledge about patterns and mechanisms that are normally studied at a larger scale (Kraft et al., 2011; Myers et al., 2013). While the link between reduced niche breadth and increased beta diversity along this microclimate gradient remains unclear, further manipulative investigations of leaf surface chemistry and propagules colonization will be able to elucidate more specific mechanisms behind this observed pattern.

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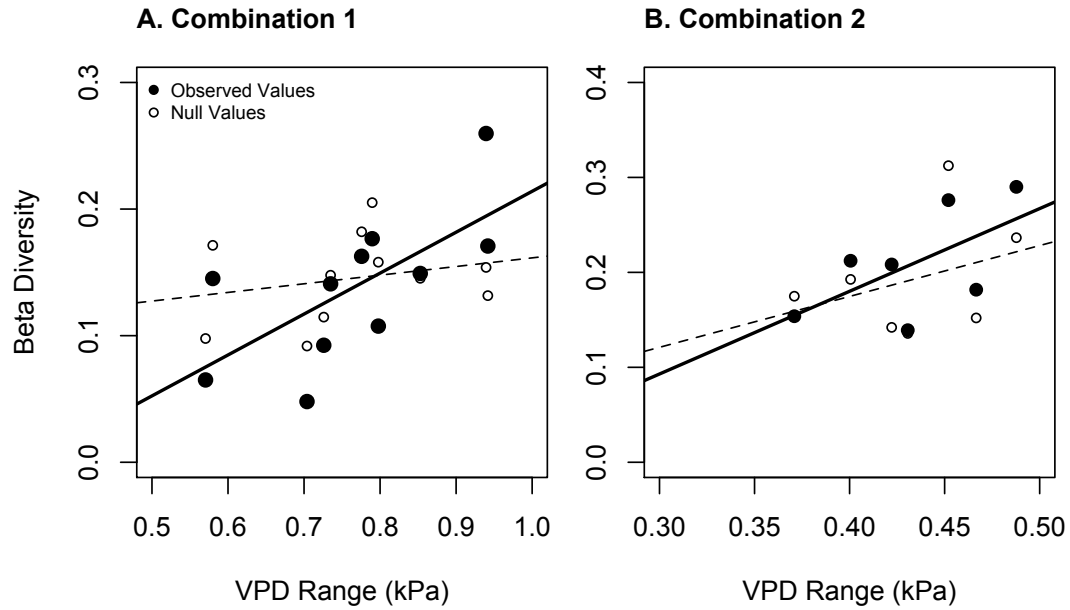


Figure 2.1: Relationship between the daily vapor pressure deficit (VPD) range and beta diversity among epiphyllous bryophyte communities on the host combination 1 (**A:** *Inocarpus fagifer*, *Bolbitis lonchophora*, *Syzygium malaccense*) and combination 2 (**B:** *I. fagifer*, *B. lonchophora*, *Teratophyllum wilkesianum*) on the island of Moorea, French Polynesia. Filled black circles represent the observed values of beta diversity, and open circle represent the values of beta diversity from null expectation (see text). Beta diversity generally increases with increasing daily VPD range (linear mixed effect model, $P = 0.01$).

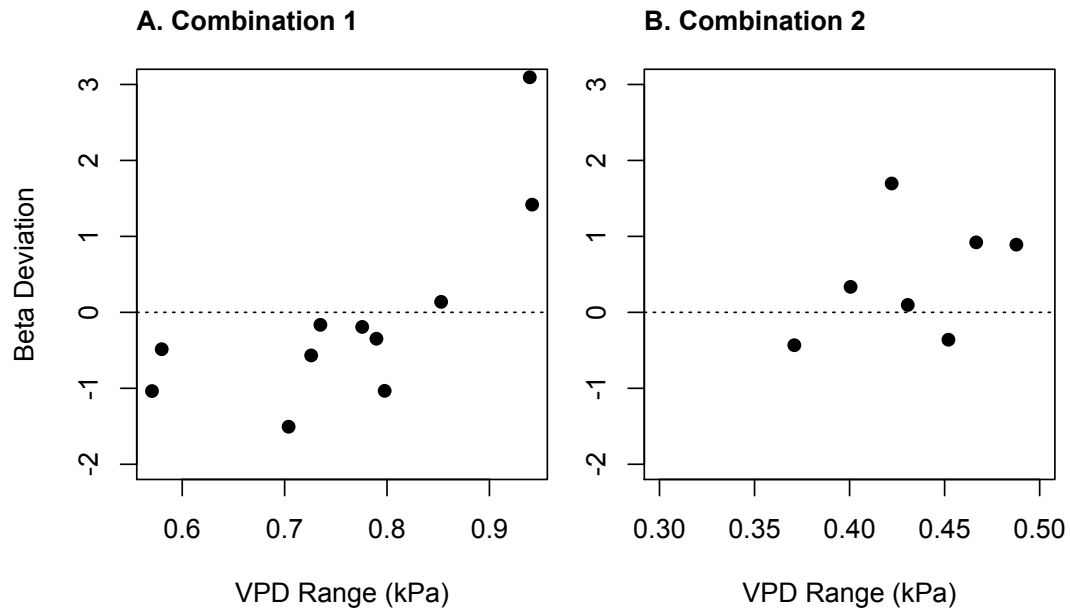


Figure 2.2: Beta deviation of epiphyllous bryophyte community communities on two combinations of host types along the daily vapor pressure deficit (VPD) range gradient on the island of Moorea, French Polynesia. Dotted lines represent the beta deviation of zero (no difference between the observed and expected values from the null model). The beta deviation is likely to be positive at the higher VPD range.

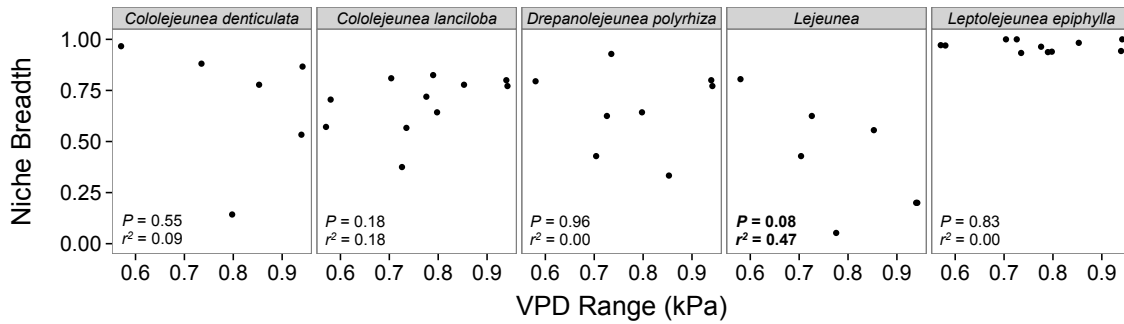


Figure 2.3: Niche breadth of five major epiphyllous bryophytes along the vapor pressure deficit (VPD) range in the host combination 1 (*Inocarpus fagifer*, *Bolbitis lonchophora*, *Syzygium malaccense*) on the island of Moorea, French Polynesia. P and r^2 values are derived from linear regression.

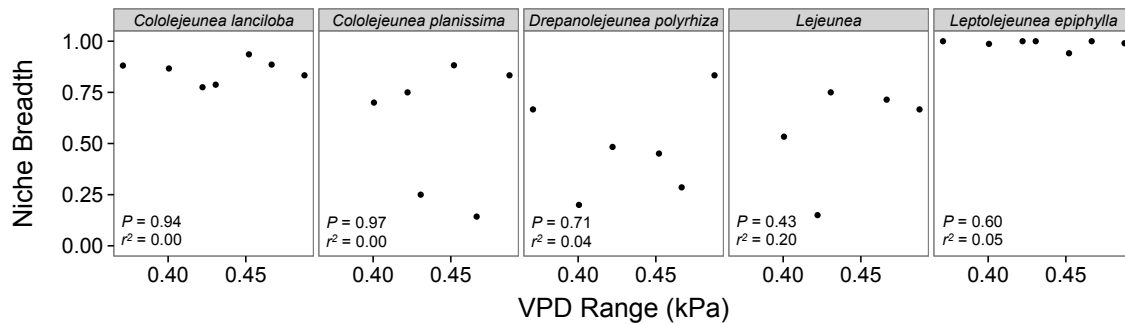


Figure 2.4: Niche breadth of five major epiphyllous bryophytes along the vapor pressure deficit (VPD) range in the host combination 2 (*Inocarpus fagifer*, *Bolbitis lonchophora*, *Teratophyllum wilkesianum*) on the island of Moorea, French Polynesia. P and r^2 values are derived from linear regression.

CHAPTER 3

Divergent Succession of Bryophytes on Leaf Surfaces

ABSTRACT

Communities of leaf-dwelling (epiphyllous) bryophytes offer unique opportunities to study succession, because each host harbors a spatially and temporally discrete community that can be obtained in large numbers for replication. In this study, I examined successional patterns of epiphyllous communities on hundreds of *Inocarpus fagifer* leaves from Moorea, French Polynesia, using both chronosequence and long-term observation approaches. Over time, species richness increased along with significant shifts in community composition. The dominant species, *Leptolejeunea epiphylla*, was found to be the common first colonizer that contributed the most to the changes in species composition. Communities on the older leaves were also more varied than those on the younger leaves, suggesting the divergent successional trajectories. These patterns suggest the role of facilitation by early successional species, as well as stochastic processes in the highly dynamic environment of the leaf surface.

Keywords: Bryophytes, Divergence, Epiphyll, Liverworts, Facilitation, Succession

INTRODUCTION

Studies of ecological succession have played an important role in advancing modern ecology, as they pull together a wide range of knowledge and understanding about the biology of organisms and their interactions (Walker and del Moral, 2008). Traditionally, succession was defined as a linear, predictable change of community composition toward a recognizable “climax” community (Clements, 1916; Pickett et al., 2009). It was also assumed that successional communities in a similar environment would eventually become more similar - or converge - over time (Peet, 1992). However, after a century of observational and experimental work, only a few cases of convergent succession have been documented in the nature, and the notion of the “climax community” has proved difficult to identify (Matthews, 1979). Instead, many cases of multiple successional trajectories and divergent succession have been reported (Lepš and Rejmánek, 1991). This more inclusive understanding of succession leads to more detailed studies on multiple trajectories and the mechanisms behind them. The knowledge gained from these works has been particularly instrumental and productive for applications in restoration ecology (Matthews and Spyreas, 2010).

For primary succession, studies of convergent and divergent trajectories have been limited by the availability of appropriate sites and the number of replications. In terrestrial vascular plants, most studies on primary succession come from only a few well-known cases, particularly the sites recovering from volcanic eruptions (e.g. Krakatao (Whittaker et al., 1989); Mount St.Helen (Wood and del Moral, 1988)). These sites require long-term observation (25+ years) in order to detect significant successional changes (del Moral and Grishin, 1999). In many cases, the use of sites of different ages (chronosequence) offers a faster alternative, but it is often confounded with spatial autocorrelations (Austin, 1981). With either of these methods, the

number of replicates is often small, making it difficult to generalize about patterns and processes of succession.

Leaf-colonizing (epiphyllous) bryophytes provide an invaluable system for the study of primary succession. Virtually all epiphyllous communities start on a new, empty leaf surface with no dormant or stored propagules, fitting the definition of primary succession. Most host leaves last about 1-4 years, making it possible to observe the entire sequence of succession within a relatively short period of time (Zartman, 2004). Moreover, leaves of different ages on the same branch or plant can serve as a proper chronosequence, because they experience more or less the same microclimate, and the observed pattern will not be confounded by spatial autocorrelation. Large numbers of epiphyllous communities can be obtained from most humid tropical forests and preserved for later studies. Despite these advantages, only a few studies have set out to specifically examine successional patterns of epiphyllous communities (Winkler, 1967; Daniels, 1998).

The current study took advantage of the abundance of epiphyllous communities on the leaves of Tahitian Chestnut (*Inocarpus fagifer*) to examine successional patterns, using both chronosequence and long-term observation approaches. More specifically, I asked the following questions: (1) Do the percent cover and species richness of epiphyllous bryophytes increase over time? (2) Does the species composition of the community change over time? (3) What are the trajectories of succession? And finally (4) Are communities converging or diverging over time? I hypothesized that percent cover and richness would increase over time, resulting in compositional changes. Similar to other studies in successional vascular plant communities (Matthews and Spyreas, 2010), these compositional shifts would also involve multiple trajectories, leading to diverging communities over time.

METHODS

Study Sites - The study was conducted on the island of Moorea (17° 29' 25" S, 149°49' 34" W). As one of the Society Islands, French Polynesia, Moorea lies roughly 17 km northwest of Tahiti with an area of 134 square kilometers. The study area was located in the mid-elevation secondary forest (118-241 m above sea level) in the Opunohu Valley, where the majority of land is protected from cultivation and tourism. Average annual precipitation of this area is 325 cm (Resh et al., 1990). After 2,000 years of extensive land use by Polynesians, the area was mostly abandoned after the European arrival in 1768 (Green et al., 1967; Lepofsky et al., 1996). The common canopy tree today species include Tahitian Chestnut (*Inocarpus fagifer*), Sea Hibiscus (*Hibiscus tiliaceus*), Malay Apple (*Syzygium malaccense*), Candlenut (*Aleurite moluccana*), and Mara (*Neonauclea fosteri*). The ancient Polynesians introduced a number of these species, including *I. fagifer*, a native to the Indo-Malaysian region. The understory layer is normally consisted of seedlings and saplings of canopy trees, as well as *Eugenia reinwardtiana*, *Freycinetia* spp., *Spathoglottis plicata*, and various ferns (*Angiopteris evecta*, *Bolbitis lonchophora*, *Teraphyllum wilkesianum*, *Lomariopsis brachenridgei*, and *Nephrolepis hirsutula*).

Chronosequence data collection - Chronosequences of epiphyllous communities on the leaves of *Inocarpus fagifer* were used as a study system, because *I. fagifer* produces new leaves in flushes of two to four, allowing rapid determination of the relative age on the same plant in the field. Each flush of leaves was approximately one to two years apart. A total of 384 leaves from 128 plants were collected from 36 haphazardly selected locations along the Three Pines and

Three Coconuts trails during September to November 2011. Three leaves from three different age classes were chosen from young *I. fagifer* saplings (< 2m high). The youngest age class at the top represented leaf age 1, and two more age classes down the stem represented leaf age 2 and 3, respectively (**Fig. 3.1**). Since epiphyllous communities on the same plant all start on the empty leaves and share a similar set of microclimatic factors, the system avoids many of the problems that confront chronosequence studies conducted over larger spatial and temporal scales. The leaf samples were pressed and dry-preserved for identification in the laboratory at University of California, Berkeley.

Identification and community assessment - The epiphyllous bryophytes were identified under the dissecting and compound microscopes. Identification and nomenclatures in this study followed the conventions in Zhu and So (2001) and Lücking (1995) and were also verified by S. R. Gradstein (Muséum National d'Histoire Naturelle, France). Voucher specimens were deposited in the UC Herbarium. Abundance of each taxon on a leaf was determined using the cover class system: 1 for 5%, 2 for 5-10%, 3 for 10-25%, 4 for 25-50%, and 5 for >50%. This cover class method has been shown to be appropriate for other cryptogamic (bryophytes and lichens) community data (McCune and Grace, 2002). Leaf area and total cover by all taxa were determined from the scanned images of the leaves using the ImageJ software (Schneider et al., 2012).

Long-term data collection - In addition to chronosequence data, 24 leaves of *I. fagifer* were randomly chosen and tagged for long-term observation. The initial abundance and composition of epiphyllous bryophytes was determined in the field in November 2011. After one year, 18 of these tagged leaves were harvested and brought back to the laboratory, as six were destroyed by a storm during the year. The identification and determination of leaf area and cover was conducted in the same manner as described above.

Chronosequence Data Analysis - The linear mixed-effect model (Lindstrom and Bates, 1988) was performed to detect the change in the percent cover and richness over time with the leaf sequence as a fixed factor and individual plant as a random factor.

To determine whether the community composition varied significantly among leaf sequences, permutational multivariate analysis of variance (PERMANOVA) was performed, using the Bray-Curtis distance matrix (McArdle and Anderson, 2001). The significant value of this test was derived from 999 permutations among leaves of the same plant. Because the Bray-Curtis distance matrix cannot directly include bare leaves (0% epiphyll cover), a dummy species with the same low abundance was added to every community (Clarke et al., 2006). The data were also transformed using Hellinger's transformation to reduce the importance of the dominant species, *Leptolejeunea epiphylla*, which had much higher abundance than other epiphyllous species in this study (Borcard et al., 2011). The shift in community composition was also visualized, using the non-metric multidimensional scaling (NMDS) with the Bray-Curtis distance from the transformed data and the maximum of 100 iterations.

To determine whether community composition was diverging or converging over time, the test for multivariate homogeneity of group dispersions (PERMDISP2 procedure in Anderson et al., 2006) was employed, using the Bray-Curtis distance. This test measures the degree of divergence by calculating the average distance of each community from the multivariate centroid of all communities in that leaf sequence. The significance value of this test was derived from 999 permutations among leaves of the same plant. In order to use the Bray-Curtis distance, the community data were transformed in the same manner as described above.

Successional trajectories were visualized by dividing all epiphyllous communities into five discrete stages, using k-means clustering. To ensure that the communities in these five stages were significantly different from each other, the PERMANOVA was also run with the clusters as the fixed factor. Then the number of transitions among these stages was calculated, separately for the transition of leaf age 1 to 2 and leaf age 2 to 3.

The mean first appearance of each epiphyllous species was also calculated by averaging the youngest leaf age at which each epiphyllous taxon appeared on each plant. A lower number represents a species that occurred mostly on the younger leaves, suggesting its role as an early colonizer or early successional species. To determine whether the regional abundance of a species affected its order of appearance, a linear regression was performed on the logarithm of number of occurrences and the mean first appearance of the species.

Long-term data analysis - changes in percent cover and richness of the epiphyllous community of the same leaf from 2011 and 2012 were tested, using paired Wilcoxon rank sum test (Bauer, 1972). The shift in community composition was visualized, using NMDS with the Bray-Curtis distance from the transformed data (as described above) and the maximum of 100 iterations. Because most of the variation occurs on the first NMDS axis, paired Wilcoxon rank sum test was performed on this first axis to determine whether the composition of epiphyllous community changed over the year. The divergence of composition over time was also determined, using the PERMDISP2 procedure with 999 permutations within each leaf.

All statistical analyses and data management were conducted in R statistical programming language (R Core Team, 2012) with additional packages *vegan* (Oksanen et al., 2012), *nlme* (Pinheiro et al., 2012), *plyr* (Wickham, 2011), *reshape* (Wickham, 2007), *picante* (Kembel et al., 2010), and *igraph* (Csardi and Nepusz, 2006).

RESULTS

Chronosequence data –The percent cover and richness of epiphyllous communities increased significantly with relative leaf ages (Linear mixed-effect model, $P < 0.0001$; **Fig. 3.2**). The majority of the cover increase could be contributed to the increase in cover of the dominant species, *L. epiphylla*. The community composition also changed significantly with leaf ages (PERMANOVA, $P = 0.001$). As the leaf age increased, the variation among communities within the same age class also increased (PERMDISP2, $P = 0.001$; **Fig. 3.3**), suggesting the divergence of communities over the course of succession.

K-means clustering analysis divided epiphyllous communities into five significantly different groups (PERMANOVA, $P = 0.001$, **Table 3.1**). The first group (BARE) consisted of mostly bare leaves and a few leaves with rare species (*Cololejeunea planissima* and *Stenolejeunea* sp.) at low abundance. The second group (CD) included leaves with mostly *Cololejeunea* species without any of the dominant species (*L. epiphylla*). The last three groups contained leaves that were *L. epiphylla*-dominated (LD) at different abundances. The LD-1 cluster had 17 percent cover of *L. epiphylla* on average with one or two additional species. Leaves in the LD-2 cluster harbored higher cover and richness of epiphylls than those in the LD-1, and finally the LD-3 clusters consisted leaves with approximately 40% percent cover and 3.38 species per leaf. Most of the leaves in the youngest age class were in the stages LD-1, LD-2, or BARE, while most of the leaves in the oldest age class were in LD-1, LD-2, or CD (**Fig. 3.4**). Multiple trajectories from each stage were found in both transitions from age 1 to 2 and 2 to 3. However, majority of

transitions occurred among the LD stages, particularly transitions within the cluster of communities.

The first appearance of *Leptolejeunea epiphylla* was mostly on the youngest leaves (age 1), whereas the rest of species were more likely to first occur on the leaf age 2 or later (**Fig. 3.5**). The mean first appearance also decreased significantly with the logarithm of total occurrences of that species. In the other words, a more abundant species was more likely to appear first on the leaf sequence (linear regression; $r^2 = 0.26$, $P = 0.02$).

Long-term data – The percent cover and richness of epiphyllous communities increased significantly over the course of the year (paired Wilcoxon rank sum test, cover $P = 0.014$ and richness $P = 0.005$; **Fig. 3.6**). The majority of the cover increase in this data set was also mainly the results of the increase in cover of *L. epiphylla*. The community composition also changed significantly from 2011 to 2012 (paired Wilcoxon rank sum test on the first axis of NMDS, $P < 0.001$, **Fig. 3.6**). However, the variation among communities in 2011 was not significantly different from that in 2012 (PERMDISP2, $P = 0.32$).

DISCUSSION

The observations from both chronosequence and long-term datasets support the hypothesis that percent cover, richness, and composition of epiphyllous bryophytes on *I. fagifer* leaves change over time. These successional changes also lead to diverging communities in the oldest age class, suggesting the existence of multiple successional trajectories in this system.

Cover Increase — The increase in percent cover in this system is mostly driven by the increase in cover of *Leptolejeunea epiphylla* over time. This species is usually the first one to colonize the leaf surface and the most abundant species in the system. This is a common pattern in early stages of primary successions, where primary colonizers – which usually have high propagule abundance and ability to disperse rapidly – quickly occupy and spread through empty space (e.g. On Mount St. Helens (Wood and del Moral, 1988)). Previous studies on epiphyllous bryophytes in Costa Rica also found the increase in the percent covers of two dominant species (*Cyclolejeunea peruviana* and *Drepanolejeunea bispinosa*) to be the main component of overall epiphyll cover (Daniels, 1998). Other studies also report an increase in epiphyll cover over time, but fail to distinguish the relative contribution of each epiphyllous species (Monge-Nájera, 1989; Coley et al., 1993; Binkowski and Nowak, 2008).

The dominance of *L. epiphylla* appears to be the result of its rapid growth. In the long-term observation, the majority of observed *L. epiphylla* patches expanded from a few percent to almost double their initial size over a year, while patches other species remained relatively the same size. A previous study on epiphylls also found that the genus *Leptolejeunea* grow sfaster in relatively drier times of the year and outcompete other fast-growing species, such as *Radula* (Olarinmoye, 1975). The growth form of *Leptolejeunea* can also contribute to this relatively rapid growth, because these plants only attach to the leaf surface at the rhizoid, where other species (especially of genus *Cololejeunea*) adhere firmly to the leaf surface at the lobe margin. While a strong attachment of *Cololejeunea* to the leaf surface may ensure establishment, it can reduce the growth rate and flexibility to highly dynamic moisture content of the leaf surface (Zhu and So, 2001).

In addition, high abundances of spores and propagules can also contribute to the dominance of *L. epiphylla*. For the current study, data on spore and propagule abundance were not systematically collected, but various forms of reproduction of *L. epiphylla* were abundantly observed in this system. This species produces a copious amount of perianths (structure enveloping female gametangia), as well as vegetative propagules, also known as “cladia” (Zhu and So, 2001). On young leaves, a large number of cladia were found scattered on the leaf surface. Small new patches of *L. epiphylla* also emerged on the leaves in the long-term observation study, suggesting colonization from propagules or spores. The mechanism of high propagule pressure is often used to explain the success of many invasive species, especially in grasslands (Lockwood et al., 2005). However, for epiphylls, a study in Costa Rica has shown that the amount of propagules available does not correspond with the observed epiphyllous communities in the same area (Daniels, 1998). While such discrepancy might be specific to that system, it is possible that the propagule pressure plays a less important role than the growth rate in early successional stages on leaf surface and subsequent expansion of the population on the leaf.

Compositional Change — With increasing cover of the dominant species, the species richness also increased, resulting in changes in the community composition over time. In the chronosequence data set, the leaves in age class 1 were mostly free of epiphylls, or contained low abundance of *L. epiphylla* (Stage BARE and LD-1). By age class 3, most of the leaves were colonized by *L. epiphylla* and several other species, such as *Cololejeunea lanciloba*, *C. denticulata*, *C. planissima*, and *Drepanolejeunea polyrhiza* (Stages LD-2, LD-3). In the long-term data set, *C. lanciloba* and *D. polyrhiza* became more common in the second year of colonization. A similar increase in species richness and shifting composition of epiphylls over time has been documented in several studies in the Neotropics and Africa (Richards, 1932; Winkler, 1967; Olarinmoye, 1975; Daniels, 1998).

It is interesting to note that the later colonizers (*Cololejeunea* spp. and *Drepanolejeunea*) have different habits and reproductive output from the dominant species. While *L. epiphylla* plants are loosely attached to the surface, the *Cololejeunea* plants are often highly appressed to the leaf surface, or to other bryophytes, and are normally found in smaller patches (2-5 mm diameter). On the other hand, *D. polyrhiza* — one of smallest epiphylls in this system — almost always grows on leaves of other bryophytes. The number of gemmae (vegetative propagules) and perianths were also fewer in these secondary colonizers (personal observation). These characteristics appear to suggest the lower ability of these species to colonize empty leaf surfaces and their dependence on the dominant species for establishment. Moreover, having a mat of bryophytes on the leaf has been shown to decrease the rate of water loss from the leaf (Berrie and Eze, 1975). Therefore, it is possible that colonies of fast growing *L. epiphylla* “facilitate” the later successional species by maintaining a moisture level on leaf surface (*sensu* Connell and Slatyer, 1977). This kind facilitative succession has been known in other systems that undergo primary succession (Chapin et al., 1994), especially in the early stages of succession (Sousa, 1979). In bryophyte-dominated systems, facilitation appears to be a major mechanism in community assembly (Økland, 1994; Mulder et al., 2001; Fenton and Bergeron, 2006). However, further manipulative experiment and extensive field data on epiphyll colonization are required to ascertain the mechanisms behind this pattern of succession.

Multiple trajectories — The predominant trajectory from relatively empty leaves to *L. epiphylla*-dominated ones was not strictly followed by every community. Multiple trajectories from any given stage were observed (Fig. 4). For example, in the chronosequence dataset, a bare leaf could either transition into the LD-1 or CD stages. The average dissimilarity among communities

of the same age class also demonstrated divergence in community structure over time, particularly from the youngest age class to the oldest age class. This divergence could be the result of spatial heterogeneity of microclimatic factors, but even plants from the same area (i.e. plants next to each other) had dissimilar communities within the same age class. In the long-term dataset, no significant divergence in composition over time was detected. This suggests that one year might not be enough time to observe the divergence of successional trajectories - a hypothesis that could also explain the lack of significant difference in the mean distance centroid within the age class 1, as compared to those within the age class 2.

Richards (1932) and Winkler (1967) reported systematic, orderly trajectories of succession among epiphylls. However, subsequent works (Olarinmoye, 1975; Daniels, 1998) have failed to find a predictable, single trajectory for their systems. The previously observed predictable succession might in fact reflect biases in interpretations. Richards provided no data or specific sequence of colonization for his assertion (1932), while Winkler (1967) reports a sequence of dominance by different genera on the leaf chronosequence. Neither of these studies explored a possibility that epiphyll succession may have multiple trajectories.

Although it deviates from the classical definition of succession, diverging successional trajectories have been repeatedly found to be fairly common among in early stages of primary successions (Matthews and Spyreas, 2010). Lepš and Rejmánek (1991) posit that divergence in succession can be derived from highly stochastic nature of early successional stages and/or facilitative mechanism, in which initial colonizers change environment over time. In their study of primary succession on Mount St. Helens, del Moral et al. (del Moral et al., 2010) attribute the causes of divergent succession to the “stressful” conditions - meaning highly variable climate factors and a great distance from the sources of propagules. A new leaf surface may also fall into this category of “stressful” habitat because of its dynamic nature (constant change in moisture and light availability) - making the colonization process highly stochastic.

The observed divergence in epiphyllous communities can also be attributed to changes in habitat qualities. Much like successions in other systems, the physical environment of the leaf surface, such as chemical composition and physical surface, can change dramatically with leaf age (Brenes-Arguedas et al., 2006). Young leaves are more likely to exude more secondary compounds as a way to defend against herbivores, while older leaves produce less of these compounds and allocate more resource to physical defense, such as hair and leaf thickness (Coley and Kursar, 1996; Brenes-Arguedas et al., 2006). These changes can occur independently from the development of the epiphyllous community. Although it is not currently known whether epiphyllous bryophytes react to these secondary compounds, a few studies have demonstrated that epiphylls do exchange nitrogen and other chemicals with the host leaf (Bentley, 1987; Wanek and Pörtl, 2005). Such exchange occurs at a low rate and might not affect the successional activity of epiphyllous bryophytes. Additionally, changes in other epiphyllous organisms, such as algae, lichens, bacteria, and fungi, can potentially affect the community structure of epiphyllous bryophytes. Abundance of epiphyllous lichens, in particular, is found to be negatively correlated with that of bryophytes (Coley et al., 1993). A detailed examination of these other epiphyllous organisms is beyond the scope of the current study and deserves further investigation.

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Table 3.1: Summary of epiphyllous communities on *Inocarpus fagifer* in five clusters, based on k-mean clustering analysis.

	BARE	CD	LD1	LD2	LD3
Number of leaves in age class 1	11	4	100	10	3
Number of leaves in age class 2	2	6	82	26	12
Number of leaves in age class 3	0	4	70	37	17
Mean Species Richness	0.15	2.00	1.25	2.49	3.38
Mean Percent Cover	0.29	5.88	17.03	25.27	40.73
Average Cover Class					
(1= a few plants to 5 = > 50%)	BARE	CD	LD1	LD2	LD3
<i>Leptolejeunea epiphylla</i>	0	0	3.07	3.52	4.16
<i>Cololejeunea lanciloba</i>	0	1.79	0	1.59	0.72
<i>Drepanolejeunea polyrhiza</i>	0	0.79	0	0.03	1.88
<i>Cololejeunea denticulata</i>	0	0.07	0.09	0.03	0.56
<i>Cololejeunea plassinima</i>	0.15	0.21	0.04	0.1	0.16
<i>Drepanolejeunea ternatensis</i>	0	0	0.02	0.08	0.12
<i>Microlejeunea punctiformis</i>	0	0.14	0.02	0.01	0.03
<i>Cheilolejeunea</i> sp.	0	0.07	0.02	0.05	0.06
<i>Lejeunea</i> sp.A	0	0	0.03	0.1	0.06
<i>Stenolejeunea</i> sp.	0.08	0	0	0.01	0.09
<i>Cololejeunea goebelii</i>	0	0	0.04	0.05	0.06
<i>Leptolejeunea maculata</i>	0	0	0.02	0.11	0
<i>Cheilolejeunea trifaria</i>	0	0.07	0	0.03	0
<i>Lopholejeunea subfusca</i>	0	0	0.03	0	0.06
Moss	0	0	0.01	0.01	0.03
<i>Cololejeunea equialba</i>	0	0	0	0.01	0
<i>Lejeunea</i> sp.B	0	0	0	0	0

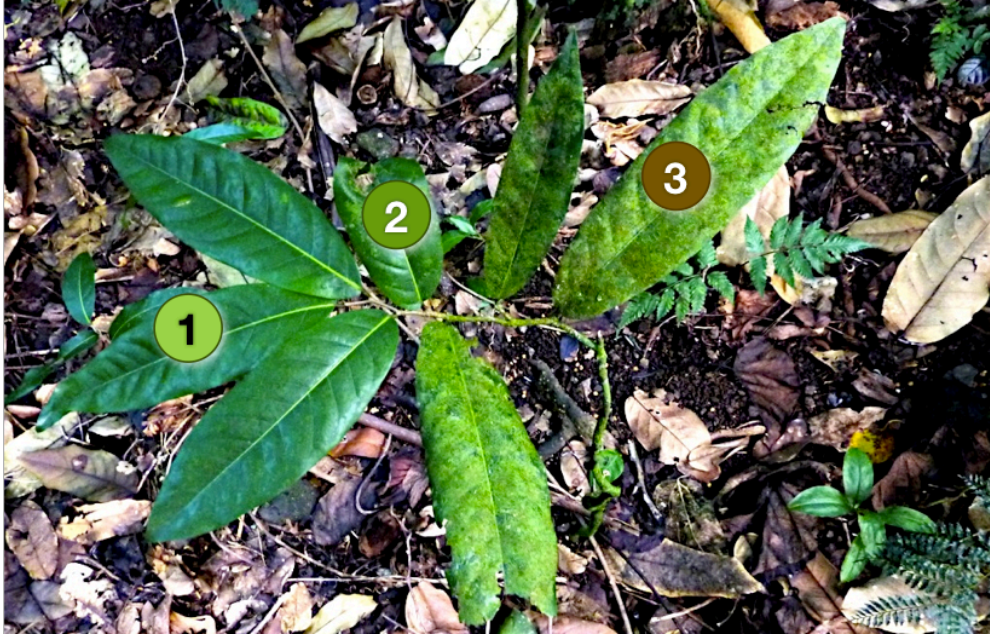


Figure 3.1: Chronosequence of *Inocarpus fagifer* leaves, based on their relative ages. The numbers indicate the age classes (1 = youngest leaf to 3 = oldest leaf).

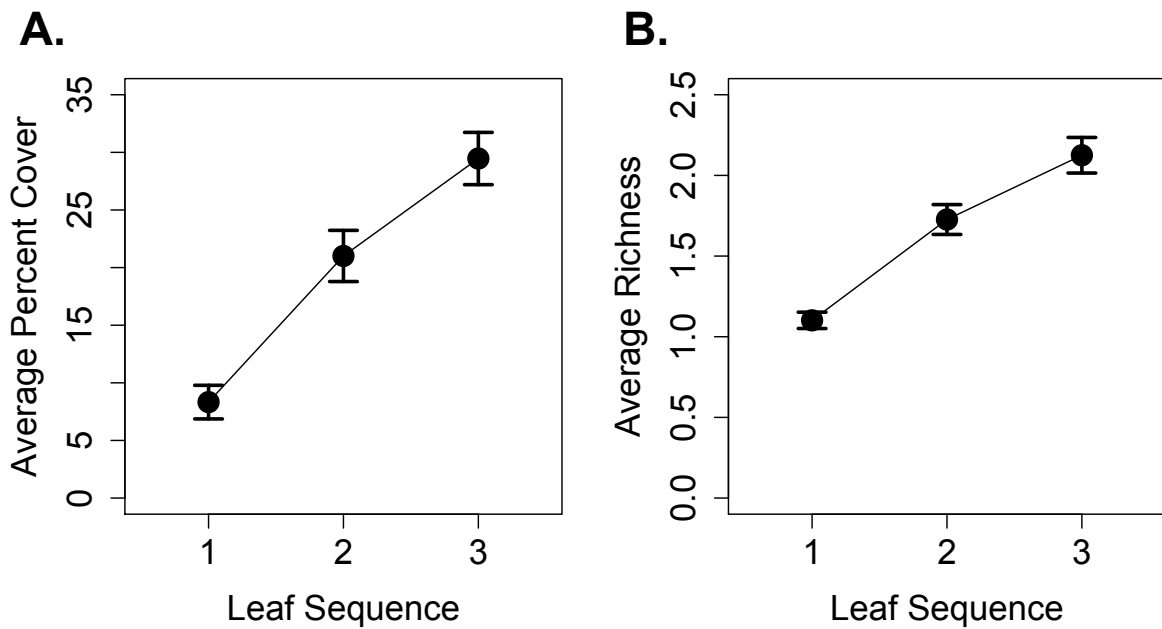


Figure 3.2: Average percent cover (A) and species richness (B) of epiphyllous bryophytes on the leaves of *Inocarpus fagifer* from different age classes (1 = youngest to 3 = oldest) on the island of Moorea, French Polynesia. Both percent cover and richness increase significantly with leaf age (Linear mixed-effect model, $P < 0.0001$)

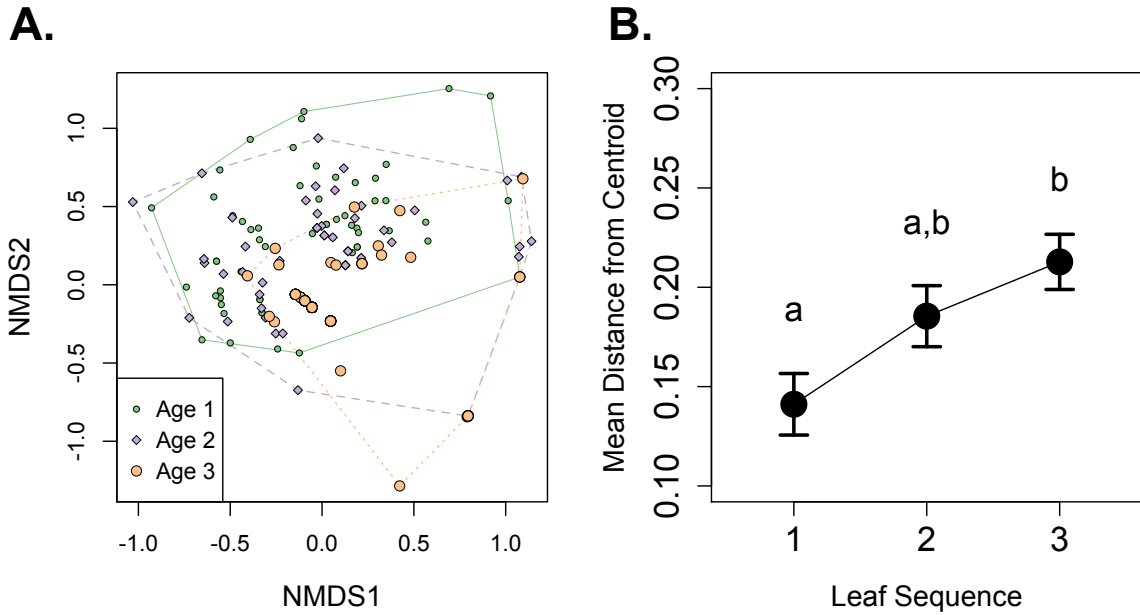


Figure 3.3: (A) First two axes of non-metric multidimensional scaling (NMDS) of epiphyllous bryophytes communities on the leaves of *Inocarpus fagifer* on the island of Moorea, French Polynesia. Each data point represents each epiphyllous community. Dotted, dashed, and solid lines represent convex hull for the epiphyllous communities on leaves in age class 1, 2, and 3, respectively. Composition shows a significant shift with the leaf age (PERMONOVA, $P = 0.001$) (B) Mean distance from the multivariate centroid of communities in each age class. The mean distance increases significantly with leaf age (PERMDISP2, $P = 0.001$).

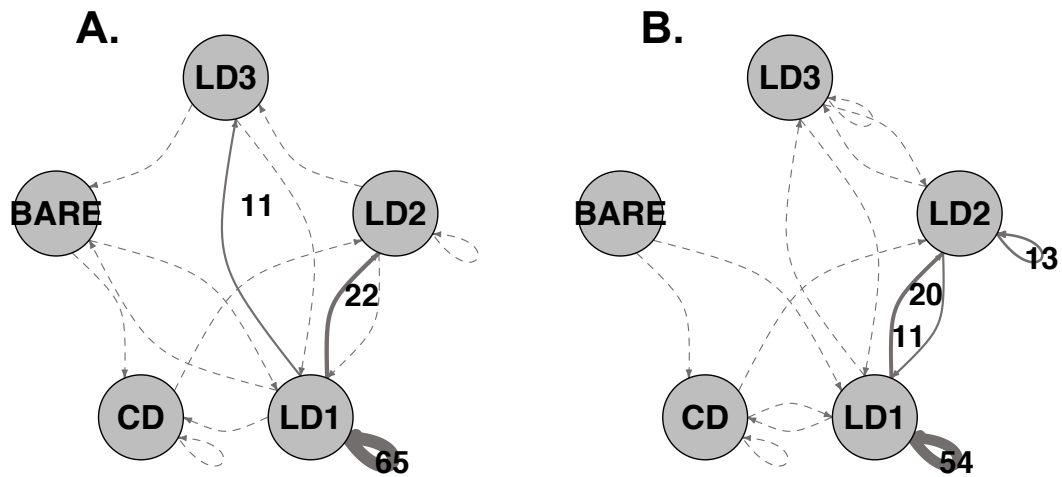


Figure 3.4: Diagram illustrating transitions among five different stages of epiphyllous communities on *Inocarpus fagifer*, as identified by k-means clustering analysis, from leaf age 1 to 2 (A.) and from age 2 to 3 (B.) Each dashed line represents a transition that occurs between 1-10 times. A solid line indicates a transition that occurs more than 10 times. The width of solid line represents the number of transitions, as indicated by the number next to it.

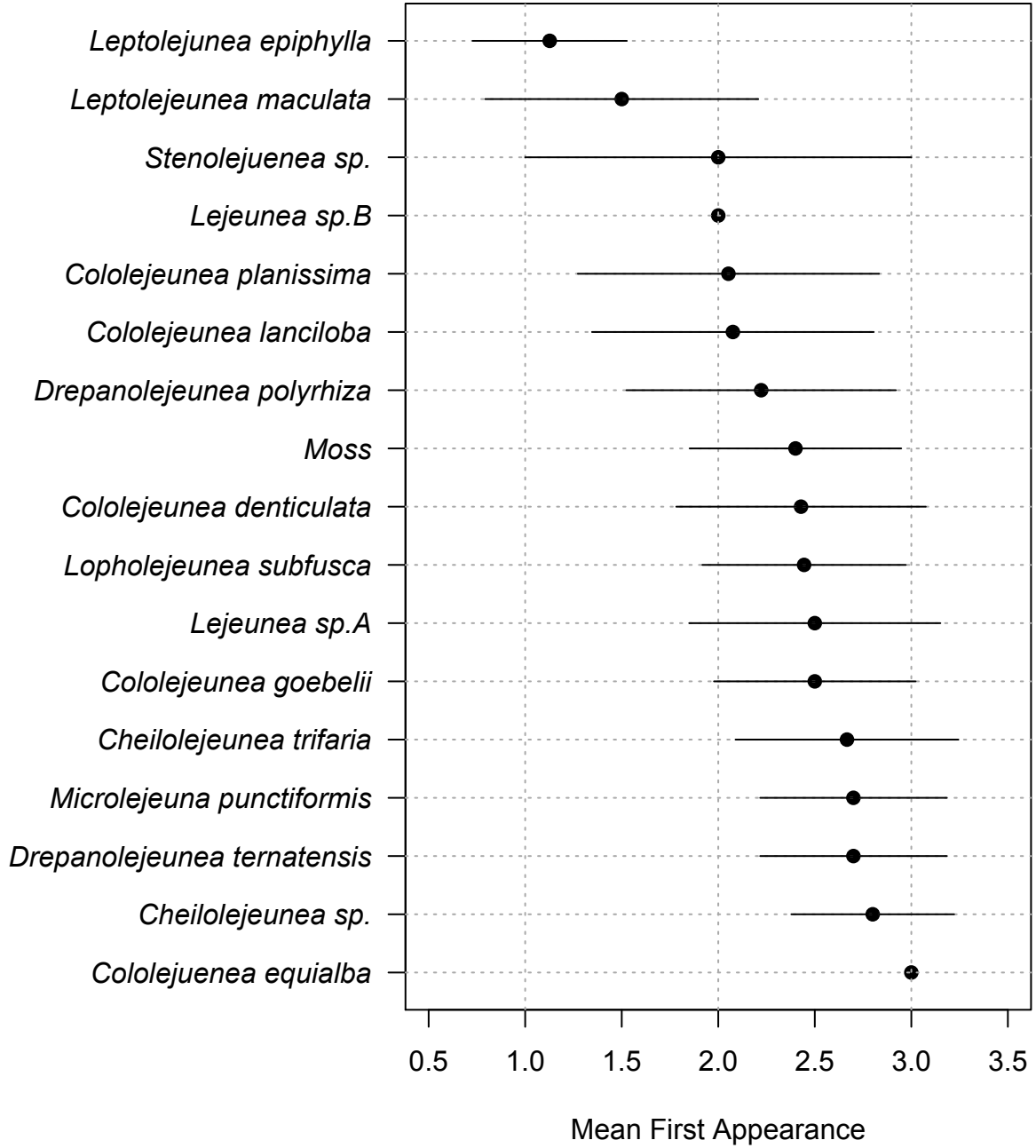


Figure 3.5: Mean order of appearance of epiphyllous bryophytes found on the leaves of *Inocarpus fagifer* on the island of Moorea, French Polynesia. The lower numbers indicate appearance in the younger age classes.

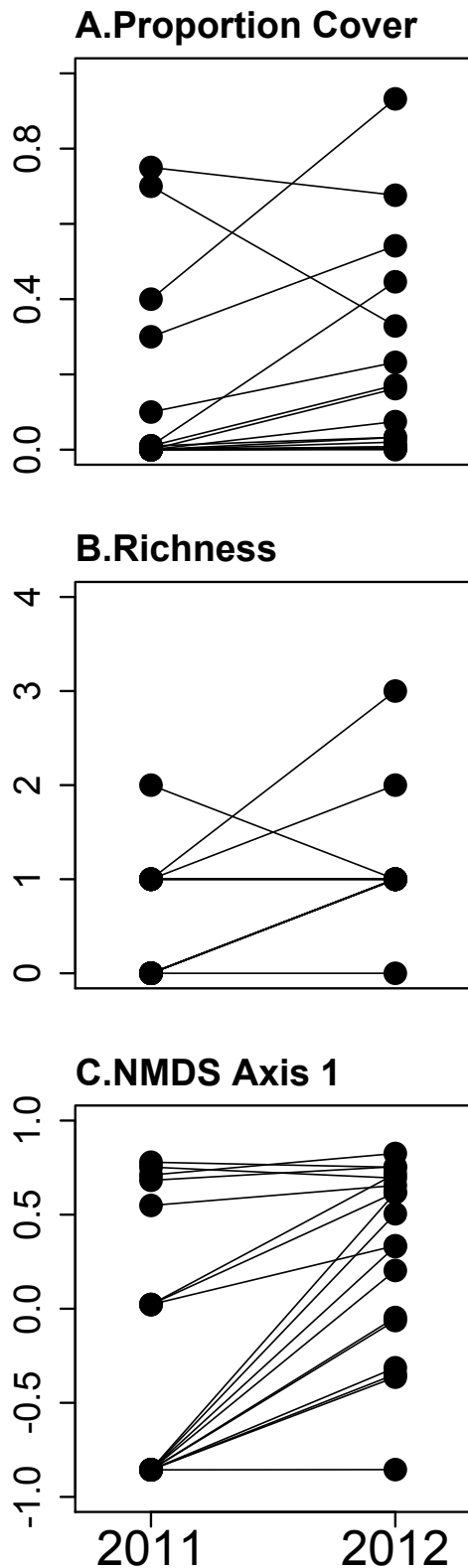


Figure 3.6: Changes in proportion cover (A), richness (B), and composition (C – represented by the first axis of NMDS) of epiphyllous communities on *Inocarpus fagifer* in the long-term observation from 2011 to 2012 on the island of Moorea, French Polynesia. Cover and richness increased significantly over the year (Paired Wilcoxon Test $P \leq 0.014$). The first axis of NMDS also exhibits significant shift between the years (Paired Wilcoxon Test $P < 0.001$).