



Are epiphytic bryophyte communities characterized by changes along an elevational gradient?—A preliminary study on eastern Viti Levu, Fiji Islands

MEREIA TABUA¹, RALPH RILEY², MATT A. M. RENNER³, LARS SÖDERSTRÖM⁴, ANDERS HAGBORG⁵ & MATT VON KONRAT⁵

¹ *Institute of Applied Science, The University of the South Pacific, Suva, Fiji*

² *Western Washington University, 516 High Street, Bellingham, WA, U.S.A*

³ *National Herbarium of New South Wales, Royal Botanic Gardens Sydney, Sydney, NSW, Australia*

⁴ *Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway*

⁵ *Gantz Family Collections Center, The Field Museum, 1400 South Lake Shore Drive, Chicago, IL, U.S.A*

Abstract

A comparative study of epiphytic bryophytes on tree trunks was undertaken in three principal vegetation types along an elevational gradient on the windward wet side of the largest island in Fiji, Viti Levu. This ecological study is the first of its kind for Fiji and the islands of the South Pacific and it serves as groundwork for any future ecological research in the region for bryophytes. This study set out to test if elevational range of study sites and height along host tree stem influenced bryophyte species diversity and distribution in Fiji. This was done by assessing bryophyte species presence/absence on the lower stems of the *Calophyllum* spp. trees and tree fern species at three elevations (~160 m, 590 m, and 1260 m). There were two main findings that emerged from this preliminary assessment. Firstly, there was a hump-shaped distribution of bryophyte diversity with a peak of species richness observed at mid-elevation or in the upland forest; with a dominance of liverworts at each of the three elevations. Secondly, the bryophyte communities showed good separation at both host tree level and at the site level, reflecting the ecological differences between the different host trees and between the three sites along the elevational gradient. The results from this survey alone suggest the need for priority to be given to upland forest protection and conservation. It also demonstrates the usefulness of bryophyte communities in discerning vegetation of different environmental and microclimatic conditions along an elevational gradient.

Keywords: *Calophyllum*, *Cyathea*, *Dicksonia*, Ecology, Pacific Islands, Liverworts, Mosses, Pacific Islands, Vegetation

Introduction

Epiphytism is often thought as a strategic survival adaptation to scarcity of water and nutrients for plant growth (van Leeerdam *et al.*, 1990). Epiphytic bryophytes are a significant component of the tropical rainforests and are known to respond sensitively to environmental changes (Frahm and Gradstein, 1991; Sporn *et al.*, 2009). They constitute important floristic and functional components of tropical rainforests and are pivotal to our understanding of forest health and integrity (Benzing, 1998) with potential usefulness as indicators of changes in microclimate (Gignac, 2001). Their diversity, however, is threatened by continued deforestation, habitat loss and modification worldwide (Söderström, 2005).

Studies on the epiphytic bryophyte diversity on trees has been investigated in many areas throughout the world, e.g., tropical America (Acebey *et al.*, 2003; Cornelissen and ter Steege, 1989; van Leeerdam *et al.*, 1990; Vital and Prado, 2006; Wolf, 1993), Africa (Pócs, 1980), Southeast Asia (Gradstein and Culmsee, 2010; Sporn *et al.*, 2010) and in cool temperate regions of Oceania (Beever, 1984; Roberts *et al.*, 2005). These studies focusing on trunk-inhabiting bryophytes have demonstrated the importance of microclimate and bark structure as a factor influencing epiphytic bryophyte distribution (Sporn *et al.*, 2010). The external texture of the substrate plays a fundamental role in retaining moisture and chemical substances, trapping spores, and supporting rhizoids (Tewari *et al.*, 2009). Also, the subtle differences in water supply, nutrients, light, microclimate regimes and inclination of the substrate affect the ability of bryophytes to establish themselves (Frahm and Gradstein, 1991; Fritz, 2009). Although there are an abundance

of ecological bryophyte studies investigating patterns in the distribution of bryophyte diversity and the relationship between elevation and bryophyte species richness, only a handful of studies have attempted this type of study on an island system.

The tropical moist forests of Fiji contain the richest and most distinct natural communities of all the oceanic islands of the Pacific, with the exception of New Caledonia (“WWF - Endangered Species Conservation | World Wildlife Fund,” n.d.), and more than 60% of the Fijian seed plant flora is considered endemic (Heads, 2006; Watkins, 1994). While the vascular flora is relatively well-documented, knowledge of the bryophyte flora of Fiji and indeed regionally for the islands of the South Pacific remains poor (von Konrat *et al.*, 2011). In an effort to further promote bryological research in the region, Söderström *et al.* (2011) presented the first ever checklist of liverworts and hornworts for the islands of Fiji.

This ecological study is the first of its kind for Fiji and the islands of the South Pacific and it serves as groundwork for any future research in the region investigating bryophyte communities. The study aimed to determine bryophyte diversity on the lower trunks of two different host tree species in three different vegetation types along an elevational gradient. It was set out to test if the elevational range of study sites and height along host tree stem influenced bryophyte species richness and distribution; that is, if the epiphytic bryophyte communities on the selected host trees reflect the changes in environmental conditions along an elevational gradient.

Methods

Study Sites:—The study was conducted on the largest island of Fiji, Viti Levu, which has a land area of 10,388 km² and on which the highest elevation of 1324 m is recorded (Kumar, 2005). All three selected sites are situated on the wet, windward side of the island along an elevational gradient. The principal vegetation types of the wet side of Viti Levu, which are also the selected vegetation types for this study, are lowland rainforest, upland rainforest and cloud forest (Mueller-Dombois and Fosberg, 1998). Specifically for the wet side of Viti Levu, the lowland rainforests are generally from sea level to roughly 600 m elevation with mean annual rainfall of 2000–3000 mm, the upland rainforests from around 600 m–900 m with mean annual rainfall of 2000–3750 mm, and the cloud forests are on the mountain peaks and ridges above 900 m and perpetually wet owing to constant cloud cover and large amount of precipitation (Mueller-Dombois and Fosberg, 1998; Watling, 2005).

The lowland site, Savura, is located around 160 m above sea level, the upland site, Namosi, 570 m above sea level, and the cloud forest site, Monasavu, 1200 m above sea level. No trees have been removed from Savura since its establishment as a reserve in 1959 (Keppel *et al.*, 2005). Namosi and Monasavu have both previously been subjected to selective logging. However it has been over twenty years for Namosi and over ten years for Monasavu since logging last took place (M. Tuiwawa & A. Naikatini, pers. comm.).

Host Trees:—Host tree selection was not species-specific but maintained at genus level to simplify site and host tree selection. A total of sixteen trees were sampled per study site, eight *Calophyllum* trees and eight tree ferns. The tree ferns (*Cyathea* and *Dicksonia* spp.) and *Calophyllum* spp. trees were chosen as host trees as they could easily be found in all three different vegetation types along the altitudinal gradient. Since bryophyte species diversity in some areas is closely associated with stem surface texture (Gradstein and Culmsee, 2010; Jansová and Soldán, 2006; Kenkel and Bradfield, 1981) it was preferred to use two host tree species that differed in stem surface texture; one smooth-stemmed and the other rough-stemmed. The stem of the *Calophyllum* trees are hard and smooth relative to the stems of the tree ferns, which are formed from layers of dense, intertwined aerial roots.

The *Calophyllum* spp. include important canopy trees that become common emergent trees, alongside other trees such as *Agathis* spp. and *Endospermum* spp., with increasing elevation. This allows them to act as cloud-filters, particularly in the upland and cloud forests. They can grow to 20 m in height and 50 cm diameter at breast height (DBH) (Smith, 1981). The *Calophyllum* trees that were sampled in this study were *Calophyllum vitiense* Turrill (1915: 17) and *Calophyllum neo-ebudicum* Guillaumin (1931: 227).

The tree ferns that were sampled were mostly *Cyathea lunulata* (Forster 1786: 456) Copeland (1929a: 37) in the lowland forest, *Cyathea decurrens* (Hooker 1844: 51) Copeland (1929b: 256) in the upland forest, and *Cyathea medullaris* Swartz (1800: 94) and *Dicksonia brackenridgei* Mettenius (1861: 81) in the cloud forest. Texture and other stem attributes may differ between tree fern species, specifically between species of *Dicksonia* and *Cyathea*. This, however, mostly affects epiphytic fern diversity rather than bryophytes, given that ferns are endohydric and are more dependent on their substrate for water and nutrients and bryophytes are primarily ectohydric (Roberts *et al.*, 2005).

Experimental design:—The three study sites were carefully selected to include sites that are situated on the wet side of Viti Levu and are protected from forest harvest by conservation agreement. The study area within each site was one hectare. Also, it was imperative that each type of host tree was located at each study site; this meant choosing host trees that could be found in the three different vegetation types—lowland, upland, and cloud forest. Literature review and preliminary fieldwork determined that both smooth-stem *Calophyllum* spp. and rough-stem tree fern spp., including *Cyathea* and *Dicksonia*, were present in all three sites.

The host trees were at least 5 m apart and those with large DBH were given first consideration since these trees would support epiphytic communities that have established over a number of years and hence would be more reflective of a more stable community. Only the lower portion of the tree trunks was chosen and these were further divided into four height zones as determined by a pre-test of the sampling method. The trees were sampled using a 10 cm x 10 cm plot in all four cardinal directions. Each individual tree was divided into four different stem height zones were demarcated using pieces of string tied around the trunk. Using a measuring tape the first zone, 0–0.5 m, was measured from the ground up. If the tree was on a slope the measurement was taken from the base of the tree that was at the highest side of the slope. The other three zones, 0.5–1 m, 1–1.5 m, 1.5–2 m, were also measured and marked by tying a string around the tree trunk at the end point of each zone. The cardinal directions of the tree trunk surface were then noted using a compass. In each zone on the trunk at each cardinal direction, two 10 cm x 10 cm plots, cut from cardboard, were randomly placed in areas within each zone. The bryophytes that fell within the 10 cm x 10 cm microplots were sampled by scraping them off the bark. A total of 1536 microplots were sampled across the three sites.

Identification & nomenclature:—Most specimens were identified to family, genus, or species level following standard practices. This included using published taxonomic identification keys, comparison to herbarium specimens or material was identified by experts. The author's citations of plant names and other abbreviations followed mainly referenced literature (Bartram, 1939; Eddy, 1996, 1990, 1988, "HathiTrust Digital Library," n.d., "Taxonomic Literature II: Smithsonian Libraries," n.d., "Tropicos," n.d.; Söderström *et al.*, 2011). All material associated with this study is vouchered and deposited at SUVA.

Data Analysis:—Using presence or absence of species, the analysis is broken down into two parts: i) analysis of taxa richness and ii) multivariate analysis of community composition. Rarefaction analysis was done at host tree species level and individual tree level. This was carried out to test for sampling efficiency and to provide an indication of community evenness. Additionally, the Sørensen similarity index was used to calculate the similarity between paired microplots, each pair within each zone within each aspect on each host tree in each site, to see how much more information the two microplots per zone per aspect per host per site gave us. Multivariate analysis of community composition was performed using the Nonmetric Multidimensional Scaling (NMDS) to graphically represent similarities of bryophyte communities on the different hosts in the different sites. The bryophyte taxa presence/absence data for individual trees was standardized by calculating Bray-Curtis similarity indices between bryophyte communities on all 48 trees sampled at the three sites on the two host tree species. To establish whether there were significant differences between the bryophyte communities of each tree, a Permutational Multivariate Analysis of Variance of the Bray-Curtis matrix was carried out. Site was used as the main factor, and host tree species was nested within site.

Rarefaction analysis was done using R version 2.15.0 (R Core Team, 2013); multivariate analysis of community composition was performed using the Non Metric Multidimensional Scaling (NMDS) in the Vegan package 2.3-1 in R version 3.2.2; and Permutational Multivariate Analysis of Variance of the Bray-Curtis matrix was carried out using the *adonis* function within the Vegan package 2.3-1 in R version 3.2.2.

Results & Discussion

Sampling efficiency:—The rarefaction analysis indicated our sampling effort adequately captured the taxa richness at the site level (Figure 1) and individual host tree level (Figure 2) since mean taxa richness levels off for both host trees at all sites as indicated by their accumulation curves.

Of the 1536 sampled microplots along the elevational gradient, bryophyte taxa recorded ranged from 0 to 15 per microplot (100 cm²). Only 718 microplots contained at least one bryophyte taxon. The mean +95% CI Sørensen similarity index for those tree zones where both 10 cm x 10 cm sampling microplots contained bryophytes was 0.54. This indicated that if only one 10 cm x 10 cm sampling microplot was used, almost 50% of the taxa richness in each tree zone would have been missed.

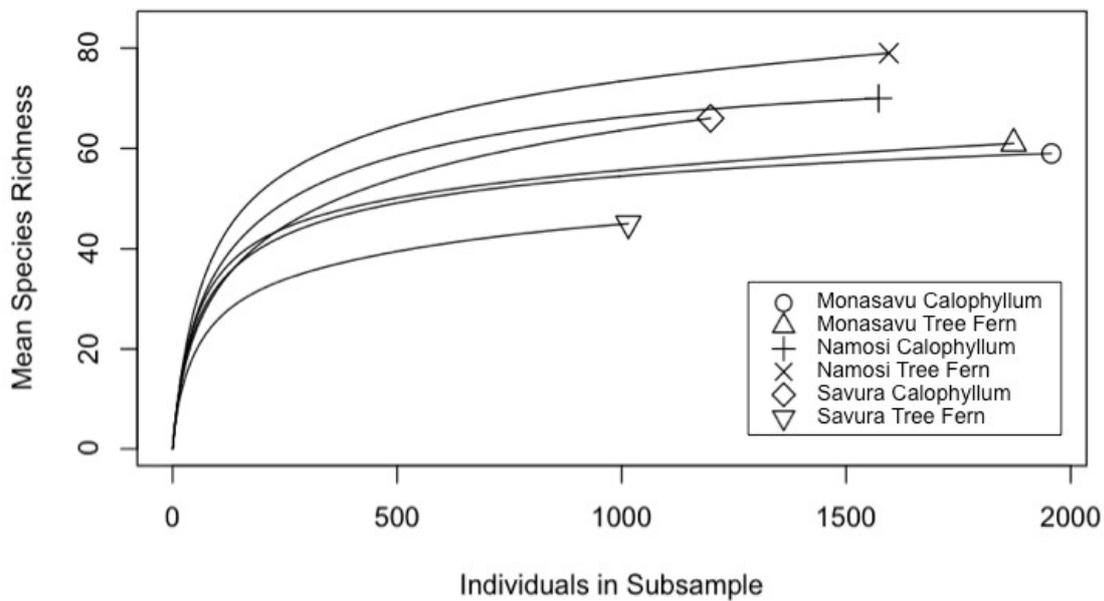


FIGURE 1. Rarefaction analysis of bryophyte species richness at the level of host tree species within each site.

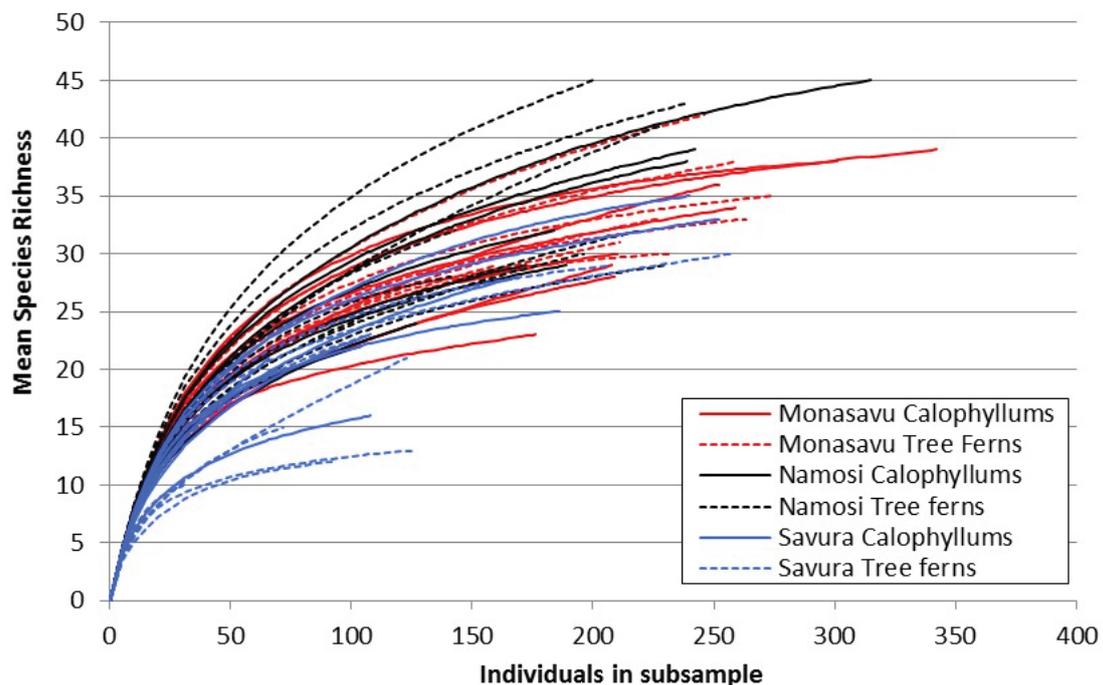


FIGURE 2. Rarefaction analysis of bryophyte species richness at the level of individual host trees within each site.

Effect of altitude on taxa richness:—143 bryophyte taxa were identified from a total of 9210 specimens. This diversity was composed of 51 mosses from 15 families and 92 (90 leafy and 2 thalloid) liverworts from 16 liverwort families. No hornworts were recorded. The observations included eight species previously unrecorded for Fiji, as well as one potentially new species to Science that is still under investigation. von Konrat *et al.* (2014) documented three of these new records; the remaining others are to be formally reported in a forthcoming paper.

There was a hump-shaped distribution of total bryophyte richness (Figure 3), total mosses, and total liverworts (Figure 4) with elevation, with a dominance of liverworts along the elevational gradient. This observed pattern is comparable to the mid-domain effect model (Colwell and Lees, 2000). That is, there was an initial increase followed by a peak in the upland forest, Namosi, then a decline with further increase in elevation. Other studies have shown similar (Ah-Peng *et al.*, 2012; Grau *et al.*, 2007; Wolf, 1993) or contrasting trends (Bruun *et al.*, 2006; Sun *et al.*, 2013; Tusiime *et al.*, 2007). While there is still no explanation for these different trends, various factors such as forest stand structure, canopy cover, forest management and climate can influence species richness, community structure and growth rate of bryophytes (Bardat and Aubert, 2007; Bergamini *et al.*, 2009; Márialigeti *et al.*, 2009; Sun *et al.*, 2013; Weibull and Rydin, 2005).

However, peak richness of bryophytes is said to coincide with high moisture levels, maximum number of rainy days and frequent cloud immersion (Bhattarai *et al.*, 2004; Frahm, 2002; Song *et al.*, 2011). Proctor (2011), however, stressed that it is the frequency rather than amount of precipitation, or the frequency of periods of 100% humidity rather than the constancy of high humidity that matters for most bryophytes. This is opposed to the common hypothesis that bryophytes are favoured by high rainfall and high relative humidity (Frahm *et al.*, 2003). The species richness reaching its peak in Namosi, the upland forest site, is consistent with this observation since rainfall recorded in 2012 was a lot higher at the upland forest site for most months and may suggest optimal conditions for bryophyte growth at that altitude. All three sites showed high relative humidity readings daily and typically high rainfall readings particularly during the cyclone season in Fiji. However the upland forest site, Namosi, recorded the highest rainfall for six months, cloud forest site for five months and the lowland site had the highest rainfall recorded for one month only (Fiji Meteorological Services, 2012). Namosi is at a higher elevation than Savura, the lowland study site, and probably receives additional orographic rainfall. Although, Monasavu, the cloud forest study site, is at a still higher elevation than Namosi, it is located further inland on Viti Levu and therefore is sheltered from the moisture-laden south east trade winds to which the upland study is more exposed. Sun *et al.* (2013) suggested that the poikilohydric properties of bryophytes may be one of the reasons air temperature, precipitation, and relative humidity influence bryophyte distribution.

Liverworts dominate diversity along the elevational gradient:—In this study, the species richness peak for the mosses was much lower than that of the liverworts along the elevational gradient (Figure 4). While both mosses and liverworts within the same site are considered to be affected evenly by environmental conditions, they exhibit different responses (Benavides *et al.*, 2004) in the epiphytic microhabitat. Furthermore, there was a gain in liverwort diversity with an increase in elevation, with species from the families Frullaniaceae, Schistochilaceae, Lepidoziaceae making an appearance at the higher elevation sites. This is in accord with other findings (e.g., Ah-Peng *et al.*, 2007; Enroth, 1990) where liverwort species increased with increasing elevation, humidity, cloud cover, and mist. Similarly, Glime and Hong (2002) demonstrated that under the right bark conditions, liverworts can be more abundant than mosses.

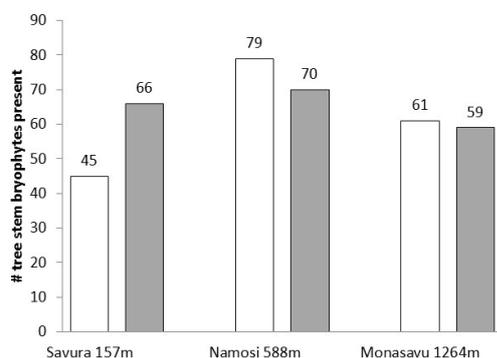


FIGURE 3. Sample-based bryophyte taxa richness by site and host tree on Viti Levu, Fiji. White bars correspond to tree ferns; grey shaded bars correspond to Calophyllum.

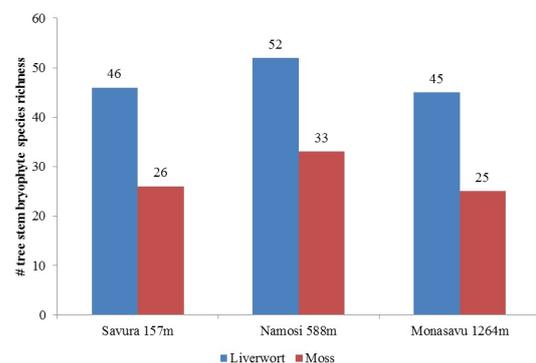


FIGURE 4. Total number of mosses and liverworts along the elevational gradient (157–1264 m) on Viti Levu (Fiji), all porophytes confounded.

Resemblance: Bray-Curtis
2D Stress: 0.1237569

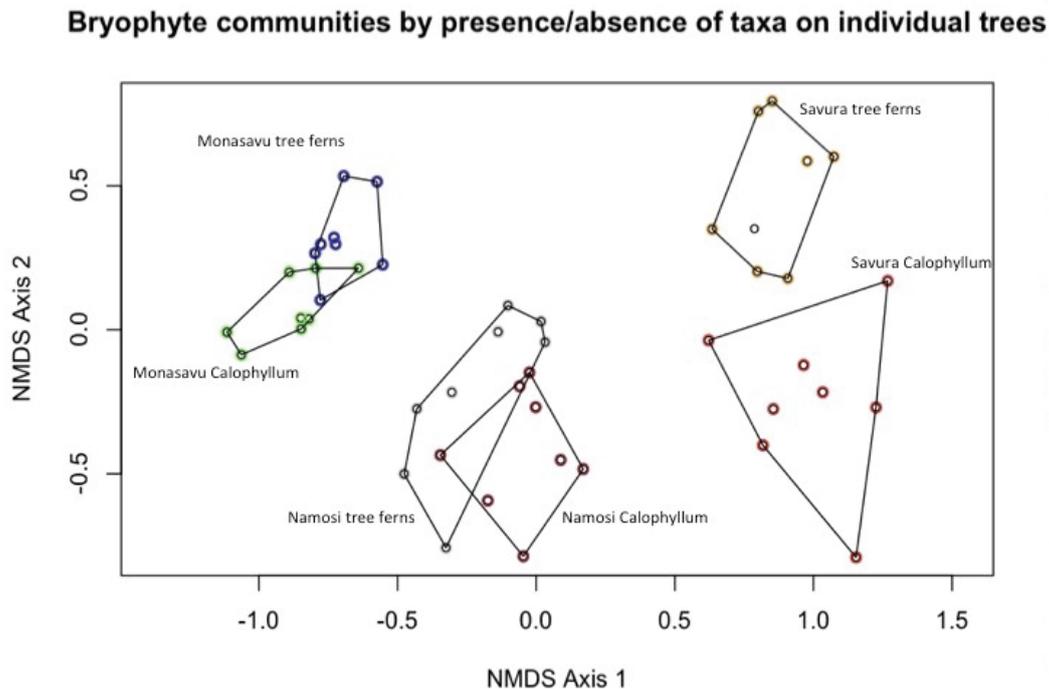


FIGURE 5. Non Metric Multidimensional Scaling (NMDS) plot showing differences in bryophyte communities based on presence/absence data for the 48 individual trees sampled at the three sites along an elevational gradient on eastern Viti Levu, Fiji. The polygons are ‘convex hulls’ that are the smallest convex envelopes which contain the data for each set of eight trees of each host tree species at the three sites; the adjacent labels indicate the site and host tree species for each convex hull.

Similarities of bryophyte communities along the elevational gradient:—The Non Metric Multidimensional Scaling (NMDS) Ordination plot in (Figure 5) graphically represents similarities of bryophyte communities on the different hosts in the different sites. This NMDS plot had a ‘stress’ value of 0.123 indicating a useful two-dimensional representation of taxa presence/absence in the bryophyte communities on individual trees (Clarke and Warwick, 2001). The NMDS plot (Figure 5) shows clear separation of bryophyte communities on trees between the three different sites indicating the bryophyte communities on individual trees are consistently different between the three sites. This interpretation is supported by the PERMANOVA which indicated a very significant difference in the bryophyte communities on trees of each of the three sites (pseudo- $F(df=2, 45)=26.641, p<0.001$).

The NMDS plot also indicates separation between the two host trees with some overlap between *Calophyllum* spp. and tree fern bryophyte communities at Namosi (upland) and Monasavu (cloud forest) but none at all at Savura (lowland). This is also reflected by the Sørensen similarity indices (Table 1) with the lowland forest, Savura, having a smaller percentage in similarity between bryophyte taxa richness on the *Calophyllum* trees versus the tree ferns. The PERMANOVA indicated a very significant difference in bryophyte communities between the two different host trees within sites (pseudo- $F(df=1, 46)=3.0369, p<0.001$).

The different bryophyte community assemblages along the elevational gradient are influenced by the different bryophyte taxa found at each study site. A possible explanation for these differences along the elevational gradient may be due to the different bryophytes responding differently to their different microclimatic conditions. Since microclimate conditions vary with altitude, differently adapted bryophytes are found at different altitudes (Sun *et al.*, 2013).

TABLE 1. Similarity between bryophyte communities on all host trees along the elevational gradient on Viti Levu, Fiji.

Site	Host	Total bryophyte taxa on all trees	Shared taxa	Taxa richness in each site	Sørensen similarity index
Savura (157 m)	<i>Calophyllum</i> Tree fern	72	39	66 45	0.70
Namosi (588 m)	<i>Calophyllum</i> Tree fern	85	64	70 79	0.86
Monasavu (1264 m)	<i>Calophyllum</i> Tree fern	70	50	59 61	0.83

Conclusion

This study has shown that altitude and its associated microclimate have a significant effect on bryophyte species richness. It has provided evidence that forests at an upland elevation are more likely to have optimal conditions for peak bryophyte taxa richness. As such this should be considered as a criterion for prioritising areas for conservation action. Also, habitat loss and canopy cover is known to negatively affect bryophyte diversity (Benítez *et al.*, 2015) and these mid elevation forests may support endemic taxa, which is mostly still unknown for Fiji.

The distinct separation of bryophyte communities in our analyses was a good reflection of ecological differences between sites along an elevational gradient as well as ecological differences between host trees. This may provide a means for monitoring change where any changes in bryophyte communities could mean a change in surrounding conditions and vice versa.

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