

Survey of Hepaticae (Liverworts) in Moorea, French Polynesia

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Abstract Interest in biodiversity is quickly increasing and lower plant groups are becoming a higher priority in conservation. However, bryophytes such as liverworts are understudied components of many ecosystems due to inadequate resources and expertise. Islands serve as model ecosystems because of their relative simplicity. The Moorea Biocode Project is an integrative survey of tropical biology on the island of Moorea, French Polynesia, collecting genetic, morphological and ecological information. Focusing on liverworts, this study investigated the species present on the island and examined ecological trends such as elevation as related to species composition and richness. Sampling was completed in the Opunohu Valley of Moorea. Sampling sites were based on known liverwort preference of moist, shaded habitats. GPS location, elevation, and host substrate were noted. Pearson's correlation was used to assess the relationship between elevation and number of samples collected per morphospecies. Overall, the study found 46 liverwort morphospecies. Some species and genera were previously documented in the literature. There were 10 new genera recorded. Elevation was found to be negatively correlated with number of samples per species, indicating a level of rarity in different habitats. However, results of this study were not consistent with richness findings of other tropical studies. Substrate observations were not significant and further examination of liverwort substrate preferences should be completed. As a preliminary targeted investigation of liverworts, this study has contributed to the current knowledge of biodiversity in Moorea. However, further studies must be conducted to obtain more information on this understudied group.

Introduction

There are an estimated 1.5 to 1.8 million species on Earth (Wilson 2003). Measuring species richness is a simplified way of examining diversity of an ecosystem and understanding community structure (MacArthur and Wilson 1967, Magurran 1988, Stevens 1989). Recognizing and understanding richness associations assist ecological studies. In particular, there is a distinct trend in plant species biodiversity, with an increasing number of species per area as latitude decreases (Dirzo and Raven 2003). Stevens (1989) found the species richness gradient of North American trees complements Rapoport's rule, which suggests range size decreases with latitude. Maximizing species richness is often a goal of conservation studies (May 1988).

Lower plant groups are becoming a higher priority in conservation (Wyatt 1992, Wolf 1993, Pharo and Beattie 1997, Kautz and Gradstein 2001). Additionally, preservation of genetic diversity has become a more important aspect of conservation biology, especially from an evolutionary perspective on population genetics (Milligan *et al.* 1994). Certain groups of bryophytes, such as mosses, exhibit genetic diversity that is comparable to higher plants taxa such as angiosperms. Although bryophyte ecology limits their robust populations to specific habitats, these habitats may be more widely distributed geographically than angiosperms (Wyatt 1992). Thus bryophyte studies can be a means of studying genetic diversity at local, regional, or worldwide distributions. Furthermore, bryophytes are important contributors to biomass in tropical and neotropical forests (Nadkarni 1984). They also have ecological roles including preventing soil erosion by colonizing dry substrates (Kürschner 2004), contributing to soil hydrology and chemistry, nutrient mineralization, and interacting with vascular plants (Cornelissen *et al.* 2007).

Altitude and host substrates are two important ecological factors that affect the make up of bryophyte communities. Liverworts in particular exhibit higher endemism at higher altitudes (Gradstein and Weber 1982). With specific regard to epiphylls, liverworts that grow on leaves of other living material, the highest instances of diversity are found in Southeast Asia and the South Pacific, specifically the regions of the Melasian Archipelago including Indonesia, and Melanesia including New Guinea and the Soloman Islands (Pócs 1996). Heylan and Hermy (2008) also found certain epiphyllous liverworts to be indicators of biodiversity in various Belgian woodland and grassland habitats, particularly after periods of significant air pollution. Past biodiversity surveys have been limited by resource availability and expertise (Wilson 1985). As a result,

bryophytes and lichens are often omitted, despite their importance. For a more complete assessment of species richness then, it is necessary to include complete bryophyte diversity for effective conservation, particularly in tropical biodiversity surveys.

One such survey is the Moorea Biocode project, which aims to provide databases with information to assist species identification, further the understanding of ecosystem interactions, and integrate taxonomy and ecology (Check 2006). In order to do this, the Biocode project seeks to collect genetic, morphological and ecological information, thus linking physical and genetic identifiers for all plant, animal, and fungal species in Moorea, French Polynesia. Islands or island groups, such as French Polynesia and Micronesia, are considered biological hotspots with many endemic species (Myers *et al.* 2000). Because of their relative simplicity, islands serve as model ecosystems for understanding the processes that drive species diversification and biological invasion (Slud 1976). Now that pilot studies have completed several vertebrate and invertebrate lineages, the current Biocode project's goals are to identify all macro species on the island, including vascular plants and non-vascular plants such as bryophytes. Of the bryophyte groups on Moorea, mosses and ferns have been well documented and studied (Ranker *et al.* 2005, d'Artenay *et al.* 2006, Nitta 2006) but nonvascular bryophytes, such as liverworts, have not (Dobbs 2006). Because the species and genetic diversity, habitat preference, and distribution of this group are largely unknown, there is a pressing need to study the variation of environmental requirements throughout a geographic range (Söderström *et al.* 1992).

As thorough sampling of Moorean liverworts has never been done, in this study I will document and examine the liverwort species found on the island of Moorea. I predict I will find both species documented in the literature as well as new species previously undocumented, particularly in unique cloud forest habitats at high elevations. By randomly sampling different substrates in habitats that are more or less favorable to liverwort growth at varying elevations, I hope to include a wide cross section of liverwort species. Identification will be based on morphological keys specific to the tropics and neo-tropics. Additionally, I will examine species trends related to elevation gradients from sampled populations.

Methods

Moorea is located approximately 17 km northwest of Tahiti, in the Society Island archipelago of French Polynesia. Because species documentation of liverworts in French Polynesia has not

been specific to Moorea, the first aspect of this project was to compile an updated comprehensive list. Because of the close geographic proximity and habitat similarity, liverworts documented in Tahiti also may have established in Moorea since the last survey. Therefore, I also included Tahitian liverworts in the list of liverworts potentially on the island of Moorea.

Sampling I conducted fieldwork in Moorea between September 27, 2008 and October 5, 2008 to confirm presence or absence of species previously documented and to look for possibly undocumented liverwort species. Sampling was concentrated in the Opunohu Valley on the interior of the island. *Inocarpus fagifer* and *Hibiscus* spp. dominated the montane cloud forests that comprised a majority of habitats sampled. At different elevations, tree species composition varied among *Inocarpus fagifer*, *Hibiscus* spp., *Metrosideros collina*, *Neonauclea forsteri* and *Spathodea campanulata*. Because of limits due to sporadic distribution and dispersal, as well as accessibility, I sampled sites of approximately 100 m² randomly along and around trails on the island. Based on known liverwort preference of moist, shaded habitats, I sampled 57 sites. Within each site, I made up to 17 mixed collections to obtain various species and a diverse population of liverworts by scraping material from different substrates. I labeled each site as a separate collecting event. Each mixed collection consisted of mixed bryophyte collections with mosses, lichens, hornworts, and liverworts growing closely together. Amount of material collected varied according to sizes of species collected; samples of large mosses were greater in volume than vouchers for liverwort epiphylls. Preliminary identifications were made in the field to the family level and noted. Other collections were morphologically distinguished using a Bausch & Lomb Hastings triplet hand lens. At each site, I recorded GPS location according to GCS World Geodetic 1984 system and elevation. To assess amount of sunlight received, I visually assessed and estimated percent of shade cover based on canopy cover. Finally, I noted host substrate and proximity to water in meters and described the surrounding habitat for each collection.

Data Analysis I identified specimens morphologically to lowest taxonomic classification using keys by Gradstein (2001), Piippo (1990), Piippo *et al.* (2002), and Scott (1986). I performed a Pearson's correlation to examine the relationship between elevation and number of samples collected per morphospecies. All data and results are available on the Moorea Biocode online database (<http://bscit.berkeley.edu/biocode>) for public and private access to assist with future taxonomic identification and ecological research.

Results

After completing a literature review, I found 16 liverwort species in 10 families documented. These species include *Cheilolejeunea trifaria*, *Dendroceros tahitensis*, *Drepanolejeunea filicuspis*, *Dumortiera hirsute*, *Frullania calcarata*, *Heteroscyphus argutus*, *Jackiella javanica*, *Leptolejeunea epiphylla*, *Lopholejeunea eulopha*, *Marchantia amboinensis*, *Mastigolejeunea humilis*, *Metzgeria furcata*, *Plagiochila viridissima*, *Radula retroflexa*, *Spruceanthus marianus*, and *Trichocolea pluma*.

In my collections on Moorea, I recorded a total of 46 morphospecies of liverworts (Table 1). Two of these have been previously documented in Moorea including *Drepanolejeunea filicuspis* and *Radula retroflexa*. Eight genera had documented collections including *Frullania* spp., *Heteroscyphus* sp., *Leptolejeunea* spp., *Lopholejeunea* sp., *Plagiochila* sp., and *Trichocolea* sp. Sixteen other morphospecies identified to genera are new records in Moorea. These include *Acanthocoleus* sp., *Archilejeunea* sp., *Bazzania* spp., *Calypogeia* sp., *Ceratolejeunea* sp., *Cololejeunea* spp., *Cyclolejeunea* spp., *Kurzia* spp., *Lepidozia* spp., and *Rhaphidolejeunea* sp. Of the 17 identified to the family level, Aneuraceae is a new record in Moorea.

Species composition of both forest habitat and bryophyte communities changed along an elevation gradient. As average elevation increased, the number of samples per species decreased (Pearson's correlation coefficient $r=0.338$, $p<0.01$, Fig. 1). Three *Bazzania* spp., *Ceratolejeunea*

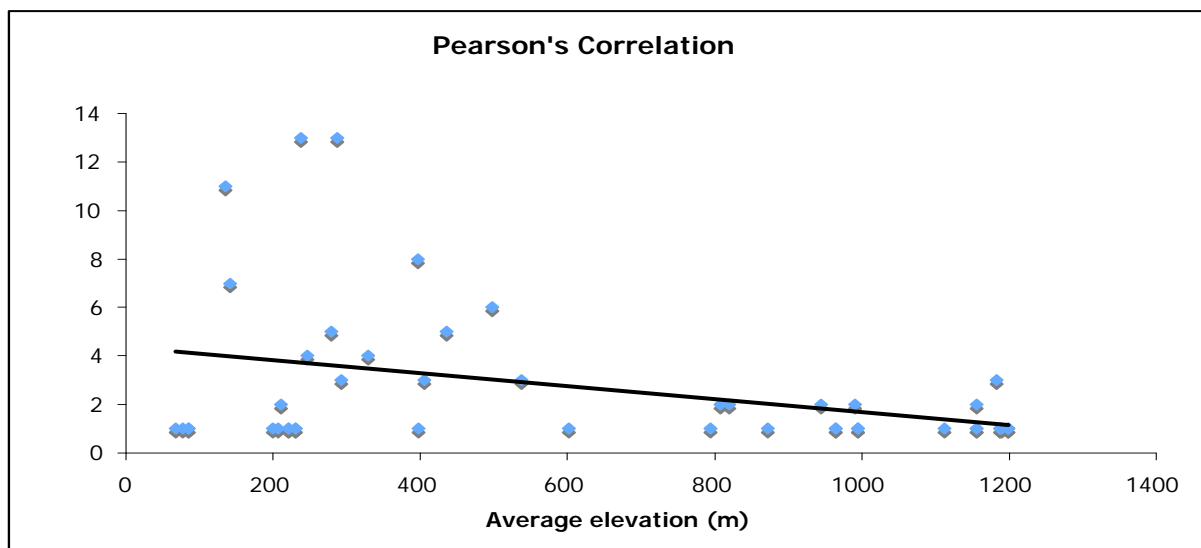


Figure 1. There was a significant decrease in the number of liverwort sampled per species as average elevation increased.

sp., 2 *Kurzia* spp., 2 *Lepidozia* spp., *Radula retroflexa*, and *Trichocolea* sp. grew only in the high elevation cloud forests of Moorea. I found 10 morphospecies to be epiphyllous liverworts in the Lejeuneaceae family, growing on leaves of *Inocarpus fagifer*, *Angiopteris* sp., *Syzygium* sp., *Asplenium* sp. and other introduced species such as ginger and bamboo. A total of 14 morphospecies grew on rock substrates such as basalt. Thirty-five species colonized bark substrates such as *Hibiscus* spp., *Neonauclea* sp., *Inocarpus fagifer* and *Metrosideros collina*.

Table 1. Liverworts of Moorea. Number of samples of each taxa collected, information on substrata (leaves – l, bark – b, rock – r, and soil – s) and average elevation.

Taxa	# collected	Substrate	Average elevation (m)
<i>Acanthocoleus</i> sp.	3	b, r	292.3
Aneuraceae	13	b, r, s	286.8
<i>Archilejeunea</i> sp.	1	b	200
<i>Bazzania</i> sp.	1	b	964
<i>Bazzania</i> sp.	2	b	807
<i>Bazzania</i> sp.	2	b	1155.5
<i>Calypogeia</i> sp.	8	b, r, l	397.1
<i>Ceratolejeunea</i> sp.	1	b	1188
<i>Cololejeuneae</i> sp.	1	r	68
<i>Cololejeuneae</i> sp.	2	b	1155.5
<i>Cyclolejeunea</i> sp.	1	l	221
<i>Cystolejeunea</i> sp.	1	b	231
<i>Drepanolejeunea filicuspis</i>	7	l	141.7
<i>Frullania</i> sp.	2	b	819.5
<i>Frullania</i> sp.	3	b, r	292.3
<i>Heteroscyphus</i> sp.	1	b	1199
Jungermanniales	2	b	990.5
Jungermanniales	1	b	1112
<i>Kurzia</i> sp.	1	b	1188
<i>Kurzia</i> sp.	2	b	944.5
<i>Lejeunea</i> sp.	1	b	872
Lejeuneaceae	5	b, r	436.2
Lejeuneaceae	1	b	994
Lejeuneaceae	3	b	537.7
Lejeuneaceae	4	l, r	246.3
Lejeuneaceae	2	l	210.5
Lejeuneaceae	1	r	398
Lejeuneaceae	13	b, r, l	237.7
Lejeuneaceae	1	r	85
Lejeuneaceae	3	b	303.7
Lejeuneaceae	1	b	231
Lejeuneaceae	3	b, r	406
Lejeuneaceae	3	b	1182.7
Lejeuneaceae	1	b	1199
Lejeuneaceae	1	b	1199

Table 1. Liverworts of Moorea continued.

Taxa	# collected	Substrate	Average elevation (m)
<i>Lepidozia</i> sp.	1	b	794
<i>Lepidozia</i> sp.	1	b	1190
<i>Leptolejeunea</i> sp.	1	l	85
<i>Leptolejeunea</i> sp.	11	l	135.3
<i>Lopholejeunea</i> sp.	5	r, b, l	279.2
<i>Plagiochila</i> sp.	6	b, r	498.3
Plagiochilaceae	1	b	964
Plagiochilaceae	1	b	994
<i>Radula retroflexa</i>	1	r	602
<i>Rhaphidolejeunea</i> sp.	1	l	221
<i>Trichocolea</i> sp.	5	b	1135.4

Discussion

With extensive sampling completed in the Opunohu Valley of Moorea and surrounding areas, this study found 2 previously documented species and adds 10 new genera and 1 new family to the recorded liverworts on the island. This amounts to 30 new morphospecies overall, expanding the list of species in Moorea compiled by Miller *et al.* (1983). Of these newly documented morphospecies, sampling in the unique habitats of high elevation cloud forests on the island found 10 potentially endemic species. Due to the isolation and fragmentation of liverwort colonies within a habitat, it is possible that speciation or genetic divergence would occur. Thus a previously documented *Frullania* sp. may in fact be a different ecotype on Moorea, particularly because this study identified two morphologically distinguishable *Frullania* species. Genetic information can further identify these species, and other morphospecies identified to genera, as well as examine how recently these species diverged. They may be recently diverged species, or previous sampling may have been unable to distinguish them from the closely related species found in other parts of French Polynesia or Oceania.

Lejeuneaceae was the most common family found, with a total of 25 species in different genera (Table 1). As Lejeuneaceae is one of the largest families found in tropical and neotropical areas, this is not a surprising result. Additionally, this family is particularly dominant in tropical forest habitats like Moorea (Gradstein *et al.* 2001). In fact, epiphytes and bryophytes with widespread continental dispersals tend to be overrepresented among island taxa (Tryon 1970). One reason is perhaps because epiphytes are adapted to constraining habitats due to their biology and morphology (Dubuisson *et al.* 2009). Furthermore, liverwort morphology

may contribute to an advantage for island establishment and colonization, as is seen with tropical epiphytic ferns (Dassler and Farrar 2001). While initially island size and available habitat may seem a constraint for establishment, such may not be the case for liverworts and other bryophyte taxa. In fact, the number of microhabitats, which liverworts often occupy, can still be correlated with high plant species richness regardless of island area (Kohn and Walsh 1994).

Of the abiotic and biotic information collected with each sample, elevation was a significant ecological factor of species distribution (Fig. 1). Past studies have found a transition zone in species composition between 400 and 500m on the island of Moorea (Meyer 2004, Nitta 2006). This study found a distinct difference in the number of samples per morphospecies collected at various elevations. At lower elevations, I collected more samples per species, indicating an abundance of relatively common species in lower montane cloud forest habitats. At higher elevations above 500m, the number of species collected per morphospecies decreased significantly, indicating a trend of species rarity as elevation increased. However, rare species still occupy habitat niches at all elevations. There were several morphospecies sampled only once at lower elevations below 400m including a Lejeuneaceae, *Leptolejeunea* sp., and *Cololejeunea* sp., *Cyclolejeunea* sp., and *Rhaphidolejeunea* sp. While other studies have found the distribution of liverwort taxa to have greatest richness within an elevation transition zone (Wolf 1993), such results were not consistent this study. This could be due to the less dramatic altitudinal gradient in Moorea as compared to the Wolf (1993) study in the Northern Andes or differences in island and continental richness trends Tryon (1970) found. While this preliminary research supports a positive correlation of beta diversity with elevation, further research investigating species turnover and varying levels of diversity would provide a better understanding of liverwort colonization and island species richness trends.

Although this study did not perform any analysis investigating substrate preference, it is nonetheless interesting to note the substrate observations. Some liverwort genera were substrate specific such as *Bazzania* and *Kurzia*, which only grew on bark, and epiphyllous liverworts such as *Drepanolejeunea filicuspis*. Yet other genera or species within a particular genus were not, including *Calypogeia* sp., *Lopholejeunea* sp. Aneuraceae species, and various Lejeuneaceae species. The wide variation within the Lejeuneaceae family is again evident in this regard. Although epiphyllous liverworts in Lejeuneaceae may specialize in niche occupancy and on leaf substrates, they are also limited by habitat and substrate availability. The number of epiphyllous

liverworts described in this study may specialize in microhabitats, as Kohn and Walsh (1994) suggested. Substrate preference studies done with mosses indicate clear preferences exist despite taxa that are generalists for substrate selection, indicating a trend in evolutionary specialization (Reese 2001). Overall, liverwort substrate preferences are not well studied or understood. Szovenyi *et al.* (2004) found species-specific relationships between epiphyllous bryophytes and substrates. Thus it is difficult to generalize trends among liverwort species and native and introduced host species. Additionally, it is difficult to predict where liverworts colonize. Although ecological and biological conditions may be appropriate, such as high relative humidity and moderate levels of shade, growth may not be abundant or even present. Hedenas *et al.* (2004) found soil composition and pH dictated most variation in species composition. Due to limited resources, this study was unable to investigate these two factors as drivers of liverwort variation and species composition in Moorea. Furthermore, although *Frullania* species colonize readily on *Hibiscus* spp. trees, not all *Hibiscus* trees have *Frullania* colonies. Additional evaluation of substrate preference should be examined due to the fact that this study did not collect complete substrate information in all samples. Specific host substrate information was not recorded for samples collected from Mt. Toheia, which has distinct cloud forest habitat not found on other parts of Moorea due to its elevation. Many of the samples collected from Mt. Toheia were above the altitudinal transition, thus there is potential for differences in substrate preference exhibited by liverworts as compared to lower altitudinal collections.

Outside of the Opunohu Valley, the island was not thoroughly sampled, thus the study is limited in its findings. It is necessary to further sample other areas of the island as well as alternate habitats to more completely document the full variety of liverworts inhabiting the island. This study collected various information for the Moorea Biocode database, however more complete information on substrate and habitat preference is needed to better understand liverwort ecology. Additionally, the use of DNA barcoding can be beneficial in further classifying and distinguishing liverwort species in Moorea. Further studies should address genetic variation within species on the island as well as phylogenetic relations between liverwort species of Moorea. Having genetic information would support morphological identification for future studies.

As a contributing study to the Moorea Biocode Project, this study demonstrated a need for targeted fieldwork to have a more complete survey of biodiversity. Morphological

identification can be further supported with genetic identification, which may be particularly useful with cryptic species. Thorough sampling for bryophytes on the island yielded a more thorough description of bryophyte taxa present, which emphasizes the need for taxonomic specialists in future biodiversity surveys.

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References

- Check E. 2006. Treasure island: pinning down a model ecosystem. *Nature* 439:378-379.
- Cornelissen, J.H.C., S.I. Lang, N.A. Soudzilovskaia, and H.J. During. 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany* 99:987-1001.
- D'Artenay, T., D.H. Norris, and B.D. Mishler. 2006. Studies on the moss flora of Moorea, French Polynesia. In press.
- Dassler, C.L. and D.R. Farrar. 2001. Significance of gametophyte form in long-distance colonization by tropical, epiphytic ferns. *Brittonia* 53: 352-369.
- Dirzo, R. and P.H. Raven. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28: 137-167.
- Dobbs, A.M. 2006. Factors influencing epiphyte habitat preference in Moorea, French Polynesia. *Biology and Geomorphology of Tropical Islands* 15: 53-64.
- Dubuisson, J.Y., H. Schneider, and S. Hennequin. 2009. Epiphytism in ferns: diversity and history. *Comptes Rendus Biologies* 332: 120-128.

- Gradstein, S.R. and W.A. Weber. 1982. Bryogeography of the Galapagos Islands. *Journal of the Hattori Botanical Laboratory* 52:127-152.
- Gradstein, S.R., S.P. Churchill and N. Salazar Allen. 2001. Guide to the Bryophytes of Tropical America. *Memoirs of the New York Botanical Garden* 86: 1-577.
- Hedenas, L., B.C. Tan, I. Bisang and C. Hammarberg. 2004. Habitat preferences in *Acroporium* (Sematophyllaceae) and related taxa in peninsular Malaysia. *The Bryologist* 107: 550-565.
- Heylen, O. and M. Hermy. 2008. Age structure and ecological characteristics of some epiphytic liverworts (*Frullania dilatata*, *Metzgeria furcata*, and *Radula complanata*). *The Bryologist* 111: 84-97.
- Kautz, T. and S.R. Gradstein. 2001. On the ecology and conservation of *Spruceanthus theobromae* (Lejeuneaceae, Hepaticae) from Western Ecuador. *The Bryologist* 104: 607-612.
- Kohn, D.D. and D.M. Walsh. 1994. Plant species richness – the effect of island size and habitat diversity. *Journal of Ecology* 82: 367-377.
- Kürschner, H. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. *Turkish Journal of Botany* 28: 73 – 84.
- MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, New Jersey. 224 pp.
- Magurran, A.E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, New Jersey. 192 pp.
- May, R.M. 1988. How many species on earth? *Science* 241: 1441-1449.
- Meyer, J.Y. 2004. Threat of invasive alien plants to native flora and forest vegetation of eastern Polynesia. *Pacific Science* 58: 357 - 375.
- Miller, H.A., H.O. Whittier, and B.A. Whittier. 1983. *Prodromus florum muscorum Polynesiae : with a key to genera*. J. Cramer, Germany. 339 pp.
- Milligan, B.G., J. Leebens-Mack, and A.E. Strand. 1994. Conservation genetics: beyond the maintenance of marker diversity. *Molecular Ecology* 3: 423-435.
- Myers N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Nadkarni, N. M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* 16:249-256.

- Nitta, J.H. 2006. Distribution, ecology, and systematics of the filmy ferns (Hymenophyllaceae) of Moorea, French Polynesia. *Biology and Geomorphology of Tropical Islands* 16: 177-199.
- Piippo, S. 1990. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXXIV. Key to the genera of Western Melanesian Hepaticae and Anthocerotae. *Annales Botanici Fennici* 27: 13-18.
- Piippo, S., X.L. He, A. Juslén, B.C. Tan, D.H. Murphy, and T. Pócs. 2002. Hepatic and hornwort flora of Singapore. *Annales Botanici Fennici* 39: 101-127.
- Pharo, E.J. and A.J. Beattie. 1997. Bryophyte and lichen diversity: a comparative study. *Australian Journal of Ecology* 22:151-162.
- Pócs, T. 1996. Epiphyllous liverwort diversity at worldwide level and its threat and conservation. *Anales Inst. Biol.Univ. Nac. Autón. Mexico, Ser. Bot.* 67: 109-127.
- Ranker, T.A., P.G. Trapp, A.R. Smith, R.C. Moran, and B.S. Parris. 2005. New records of lycophytes and ferns from Moorea, French Polynesia. *American Fern Journal* 95:126-127.
- Reese, W.D. 2001. Substrate preference in Calymperaceae: *Calymperes*, *Mitthyridium*, and *Syrrhopodon*. *The Bryologist* 104: 582-592.
- Scott, G.A.M. 1985. *Southern Australian Liverworts*. Commonwealth of Australia, Canberra. 216 pp.
- Slud P. 1976. *Geographic and climatic relationships of avifaunas with special reference to comparative distribution in the Neotropics*. Smithsonian institution Press, Washington DC. 149 pp.
- Söderström, L., T. Hallingbäck, L. Gustafsson, N. Cronberg, and L. Hedenäs. 1992. Bryophyte conservation for the future. *Biological Conservation* 59: 265-270.
- Stevens, G.C. 1989. The latitudinal gradient in geographic range: how so many species coexist in the tropics. *American Naturalist* 133: 240-256.
- Szovenyi, P., Z.S. Hock and Z. Toth. 2004. Phorophyte preferences of epiphytic bryophytes in a stream valley in the Carpathian Basin. *Journal of Bryology* 26: 137-146.
- Tryon, R. 1970. Development and evolution of fern floras of oceanic islands. *Biotropica* 2: 76-84.
- Vanderpoorten, A. and P. Engels. 2003. Patterns of bryophyte diversity and rarity at a regional scale. *Biodiversity and Conservation* 12: 545-553.
- Wilson, E.O. 1985. The biological diversity crisis: a challenge to science. *Issues in Science and*

Technology 2: 20-29.

Wilson, E.O. 2003. The encyclopedia of life. *Trends in Ecology & Evolution* 18:77-80.

Wolf, J.H.D. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the Northern Andes. *Annals of the Missouri Botanical Garden* 80: 928-960.

Wyatt, R. 1992. Conservation of rare and endangered bryophytes: input from population genetics. *Biological Conservation* 59: 99-107.