

Diversity and biogeography of Madagascan
bryophytes with an analysis of taxic and
functional diversity along an elevational
gradient in Marojejy National Park

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Abstract

A central goal of ecology is to understand the influence of biodiversity on ecosystem functioning and the processes that determine the composition and diversity of biological assemblages. In this thesis, I investigate the regional and global context of the bryophytes of Madagascar, an ecologically important but poorly studied group, and the factors affecting epiphytic bryophyte diversity, distribution and assemblage of communities along an elevational gradient in Marojejy National Park, north-eastern Madagascar.

Firstly, based on literature reviews and available herbarium data, I examined the bryophytes of Madagascar through a historical, floristic and phytogeographic synthesis. Secondly, the ecological survey of bryophytes from a range of diversity and functional perspectives provided insight on: (1) the pattern of species richness and range-size distribution of epiphytic bryophytes and the factors affecting the distribution patterns. (2) The variations in species composition between sites. I documented how the two components of beta-diversity (turnover and nestedness) are influenced by elevational variation. (3) The relationship between bryophyte species functional diversity and community assembly based on a morphological trait-based approach. I tested how bryophyte species functionally interact with their abiotic and biotic environments and how habitat filtering and niche differentiation influence bryophyte assemblages along an elevational gradient.

The bryoflora of Madagascar, with its 1188 species and infraspecific taxa is relatively rich and highly diversified. Along the Marojejy elevational gradient, 254 epiphytic bryophytes species including 157 liverworts and 97 mosses were reported. Species richness distribution has a hump-shaped pattern along the elevational gradient, with a richness peaking at mid-elevation, 1250 m. My results suggest that mid-domain-effect was the most effective in predicting species richness, but environmental variables such as mean temperature, relative humidity, vapour deficit pressure and canopy height also play important roles in shaping richness pattern. Throughout the gradient, species dissimilarity due to replacement (species turnover) contribute the most to variation in species composition between sites. Both habitat filtering and niche differentiation were found to be involved in structuring species abundances within the studied communities.

This combination of biogeographic, taxic, and community ecology approaches, is the first detailed study on the bryoflora of Madagascar and contributes to the direct application of bryological data to conservation planning for Madagascar's unique ecosystems.

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Contents

Abstract	v
Acknowledgments.....	vii
1. General introduction	3
1.1. Broad biodiversity patterns and their drivers.....	3
1.2. Feature and functional diversity - beyond species richness.....	5
1.3. Madagascar – a highly threatened hotspot of biodiversity	6
1.4. Bryophytes, a poorly known group in Madagascar	11
1.5. Objectives, research questions and thesis outline.....	14
2. An historical overview of bryology in Madagascar	19
2.1. Introduction.....	19
2.2. Bryophyte collectors and expeditions.....	20
2.3. Bryophyte collections in the National Herbarium of Madagascar (TAN).....	24
2.4. Bibliographic review.....	25
2.5. Conclusion	27
3. The Regional and Global Context: floristic and phytogeographic analysis of the bryophyte flora of Madagascar	31
3.1. Introduction.....	31
3.2. Materials and Methods.....	32
3.3. Results.....	33
3.3.1. Species diversity	33
3.3.2. Species endemism	37
3.3.3. Phytogeographic pattern of the bryophytes of Madagascar	40
3.3.4. Comparison between Madagascar and its neighbouring islands.....	44
3.4. Discussion.....	46
3.4.1. Place of the bryoflora in the Flora of Madagascar	46
3.4.2. Phytogeographic affinities of the bryophytes of Madagascar	49
3.4.3. Threats and conservation needs.....	50
4. Species richness and range distributions of epiphytic bryophytes along an elevational gradient in Marojejy National Park (Madagascar)	55
4.1. Introduction.....	55
4.2. Materials and Methods.....	57
4.2.1. Study area	57

4.2.2.	Bryophyte sampling and identification.....	60
4.2.3.	Climatic data and vegetation sampling.....	61
4.2.4.	Data analyses	61
4.3.	Results.....	66
4.3.1.	Species composition	66
4.3.2.	Bryophytes species richness pattern along the elevational gradient.....	68
4.3.3.	Species range distribution and variation along the gradient.....	70
4.3.4.	Null-model predictions	71
4.3.5.	Relationship between environmental variables and species richness pattern	73
4.4.	Discussion	75
4.4.1.	Sampling efficiency and species range interpolation	75
4.4.2.	Species composition and richness pattern	76
4.4.3.	Spatial and environmental factors	77
4.4.4.	Conclusions	79
5.	Diversity partitioning and community structure of the epiphytic bryophytes of the Marojejy National Park.....	83
5.1.	Introduction.....	83
5.2.	Materials and Methods.....	85
5.2.1.	Study area and data collection	85
5.2.2.	Data analyses	85
5.3.	Results.....	88
5.3.1.	Sample-based accumulation curves.....	88
5.3.2.	Additive partitioning of bryophyte diversity	89
5.3.3.	Effect of nestedness and species turnover on the total diversity.....	93
5.3.4.	Pairwise dissimilarity among plots.....	95
5.4.	Discussion	99
5.4.1.	Small sample size can affect completeness of sampling for epiphytic bryophytes.....	99
5.4.2.	Additive partitioning of biodiversity	99
5.4.3.	Turnover and nestedness in species composition	101
5.4.4.	Vapour pressure deficit, relative humidity and bryophyte community assembly.....	102
5.4.5.	Vegetation stage and composition of the bryoflora of the Marojejy National Park	102

6. A trait-based approach to assessing functional responses of epiphytic liverworts to environmental gradients	105
6.1. Introduction.....	105
6.2. Materials and Methods.....	107
6.2.1. Study site and data collection	107
6.2.2. Trait selection and values	107
6.2.3. Data analyses	108
6.3. Results.....	111
6.3.1. Floristic and functional diversity of epiphytic liverworts along the elevational gradient.....	111
6.3.2. Variation in community trait means along the elevational gradient.....	112
6.3.3. Effect of environmental variables on community trait means along the elevational gradient	115
6.3.4. Habitat filtering along the elevational gradient	116
6.3.5. Trait divergence along the elevational gradient	116
6.4. Discussion	119
6.4.1. Functional evenness, functional dispersion and floristic composition	119
6.4.2. Trait variation at different ecological scales.....	119
6.4.3. Habitat filtering and niche differentiation	120
6.4.4. Conclusions	123
7. General Discussion.....	127
7.1. The bryoflora of Madagascar.....	128
7.2. Community assembly and epiphytic bryophyte distribution	129
7.2.1. Diversity and distribution pattern	129
7.2.2. Deconstruction of diversity components	131
7.2.3. Implication for conservation.....	133
7.3. Perspectives and future research.....	133
7.4. Concluding remarks	135
Literature Cited	137
Appendix	175

List of figures

Figure 1: Madagascar and the Indian Ocean islands Hotspot of biodiversity	6
Figure 2: Bioclimatic regions of Madagascar (Cornet, 1974)	9
Figure 3: Vegetation of Madagascar (Du Puy & Moat, 1996)	10
Figure 4: State of identification of Bryophyte specimens in TAN.....	25
Figure 5: Liverwort species richness by family.....	35
Figure 6: Moss species richness by family.....	36
Figure 7: Distribution of endemic species across bryophyte families.....	37
Figure 8: Distribution of endemic liverwort and moss species across genera in Madagascar.....	39
Figure 9: Phytogeographical distribution of the bryophyte flora of Madagascar.....	41
Figure 10: Phytogeographic pattern for mosses and liverworts.....	41
Figure 11: Comparison of species richness and endemism between bryophytes and vascular plants.....	47
Figure 12: Movement of bryophytes from and into Madagascar.....	50
Figure 13: Location of Marojejy National Park, North-eastern Madagascar.....	58
Figure 14: Bryophytes sampling design from Ah-Peng et al. (2007), illustrated in Gabriel, Coelho, et al. (2014) (transect from low altitude to the summit).....	60
Figure 15: Numbers of microplots (50 cm ²) and number of identifications made at each elevation.....	66
Figure 16: Proportion of sampled microhabitat TA (0-50 cm), TB (50-100 cm) and TC (100-200 cm).....	67
Figure 17: Cumulative number of species (y-axis) plotted as a function of the cumulative number of samples (x-axis), pooled in random order.....	67
Figure 18: Species richness per elevational interval of 200 m for all species, mosses, and liverworts with second order polynomial trend lines (grey dotted lines).....	68
Figure 19: Species richness per elevational interval of 200 m for the different microhabitats	69

Figure 20: Elevational pattern of observed species richness (open diamond) and richness estimates (filled diamond) with standard deviation of epiphytic bryophytes along the elevational gradients.	69
Figure 21: Elevational range profiles of the 157 liverwort species collected on the Marojejy elevational gradient.	70
Figure 22: Elevational range profiles of the 97 moss species collected on the Marojejy elevational gradient.	71
Figure 23: Mean range size as function of range midpoint for epiphytic bryophytes on the Marojejy elevational gradient.	71
Figure 24: Null model predictions generated by a Monte Carlo procedure based on 50000 simulations (without replacement) of empirical range sizes using the mid-domain null program (McCain, 2004) for testing the mid-domain effect (MDE).	72
Figure 25: Species accumulation curves showing the total number of species in a given number of plots, among microhabitats (50 cm ²), quadrats (4 m ²), plots (100 m ²) and elevations (every 200 m).	88
Figure 26: Additive diversity partitioning of (a) species richness, (b) the Shannon index of diversity and (c) the Simpson index of diversity into diversity components across sampling scales: α_1 (microplots), β_1 (microplots), β_2 (quadrats), β_3 (plots) and β_4 (elevations).	90
Figure 27: Additive diversity partitioning of species richness (a), the Shannon index of diversity (b) and the Simpson index of diversity (c) into diversity components across sampling scales at each elevation: α_1 (microplots), β_1 (microplots), β_2 (quadrat) and β_3 (plots) for all epiphytic bryophytes.	91
Figure 28: Partition of the multiple-site Sørensen dissimilarity (β_{SOR}) onto its components of turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) similarity for the Marojejy elevational gradient.	93
Figure 29: Density plots representing the distribution of (a) nestedness-resultant (β_{SNE}) and (b) the turnover (β_{SIM}) across 1000 samples.	94
Figure 30: Partitioning of the multiple-site Sørensen dissimilarity (β_{SOR}) onto its components of turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) at each studied elevation for All Species, Mosses and Liverworts.	94

Figure 31: Among-elevation bryophyte species turnover at Marojejy National Park. Cluster analysis derived from the Sorensen dissimilarity $\beta_{\text{pair-sor}}$	95
Figure 32: Pattern of Functional Diversity components with elevation. A: Functional evenness, B: Functional dispersion..	111
Figure 33: Linear regression between functional diversities and species richness. A: Functional evenness, B: Functional dispersion.	112
Figure 34: Distribution of community-weighted means (CWM) by elevation (circles) and values estimated by linear models from climatic variables (grey).	113
Figure 35: Distribution of community-weighted means (CWM) of traits along the elevational gradient.....	117
Figure 36: Distribution of community-weighted variances (CWV) of traits along the elevational gradient.....	118
Figure 37: Schematic summary of the trends in functional community structure observed for eight functional traits along the elevational gradient.	122
Figure 38: Conceptual framework of the thesis.....	128

List of tables

Table 1: List of published checklists of the bryophytes of Madagascar: species recorded by authors.	27
Table 2: Distribution of Madagascan bryophyte species among nine phytogeographic groups.	40
Table 3: Comparison of the bryophyte species richness and endemism between the Indian Ocean Islands.....	45
Table 4: Matrix of Jaccard's Similarity index, comparing Madagascar, Rodrigues, Mauritius, La Réunion and Comoros.	45
Table 5: Description of environmental conditions at each plot along the elevational gradient in the Marojejy National Park.	65
Table 6: Multiple General Linear Regression (GLM) analyses of species richness against environmental variables for the overall species, mosses and liverworts.	74
Table 7: Second order polynomial regression analysis.	75
Table 8: Comparisons of observed (Obs) and expected (Exp) diversity from the null model based on 999 randomizations on species richness, the Shannon index and the Simpson's index of diversity..	92
Table 9: Results of multivariate ANOVA based on the pairwise Sørensen dissimilarity between two communities $\beta_{\text{pair-SOR}}$. with 999 simulations.	97
Table 10: Results of multivariate ANOVA based on the pairwise Sørensen dissimilarity between two communities $\beta_{\text{pair-sim}}$ and $\beta_{\text{pair-sne}}$. with 999 simulations.....	98
Table 11: AIC for models of CWM with elevation.....	114
Table 12: Regression coefficients for CWM models with elevation.....	114
Table 13: Regression coefficients for linear models of CWM with environmental variables.	115

CHAPTER 1
General introduction

1. General introduction

Human activities have strongly affected local and global environments, leading to dramatic changes in biotic structure and composition of biological communities and causing a general decline in diversity (Chapin *et al.*, 2000; Loreau & Hector, 2001; Western, 2001; Hooper *et al.*, 2005). The awareness that human survival depends on ecosystem services has made understanding of the processes responsible for generating and maintaining biological diversity and associated functional variation an important topic in ecology (Hooper *et al.*, 2005; Loreau, 2010).

It is now recognised that biodiversity affects both the dynamics and the functional scope of both communities and ecosystems (Hooper *et al.*, 2005; Cardinale *et al.*, 2012; Tilman *et al.*, 2014). For instance, biodiversity loss causes reductions in biomass production, biological resources and nutrient retention (Cardinale *et al.*, 2007; Liang *et al.*, 2015). In contrast, higher biodiversity increases the sustainability of assemblages and functioning of ecosystems (Loreau & Hector, 2001; Hooper *et al.*, 2005; Cardinale *et al.*, 2012; Tilman *et al.*, 2014). It is also clear that variation in the functional characteristics of organisms, rather than the numbers of species *per se*, has a large impact on ecosystem processes (Tilman *et al.*, 1997; Naeem & Wright, 2003; Hooper *et al.*, 2005; Hillebrand & Matthiessen, 2009).

In this thesis, I examine the diversity of bryophytes, an ecologically important but poorly studied group, from a range of diversity and functional perspectives. The study focuses on epiphytic bryophytes in Marojejy National Park, Northern Madagascar.

1.1. Broad biodiversity patterns and their drivers

The distribution of biodiversity varies heterogeneously across the earth, with a high proportion of terrestrial and freshwater species concentrated in the tropics (Gaston, 2000). Numerous studies on the distribution of terrestrial species have shown a clear and coherent pattern of diversity with respect to latitude, with biodiversity generally increasing from the poles to the equator. This pattern, referred to as the latitudinal diversity gradient, has been considered one of the most obvious worldwide patterns of species diversity. It is consistent across numerous groups, including terrestrial plants (Qian *et al.*, 2007; Qian, 2008), amphibians (Wiens *et al.*, 2009), birds (Hawkins & Diniz-Filho, 2002; Hawkins *et al.*, 2006, 2012), insects (Condamine *et al.*, 2012), mammals (Buckley *et al.*, 2010; Hawkins *et al.*, 2012) and microorganisms (Fuhrman *et al.*, 2008). However, notable exceptions to this

classical biogeographical pattern are shown by a range of different taxonomic groups, such as parasitic worms of small mammals (Krasnov *et al.*, 2008) and gymnosperms (Mutke & Barthlott, 2005), both of which show increased diversity at higher latitudes. The latitudinal pattern of species richness is driven by the systematic spatial variation in the balance of species appearance (speciation and immigration) and disappearance (extinction and emigration) (Gaston, 2000). Many hypotheses (ecological, evolutionary and historical) have been proposed to explain this pattern. One ecological explanation invokes increasing dispersal rates from temperate to tropical regions and lower dispersal rates from tropical to temperate regions. Temperate species, due to evolving under harsh and variable climatic conditions, may have broader tolerances than tropical species, and thus a wider potential dispersal range (Lyons & Willig, 2002). In contrast, tropical species, which often occupy smaller ecological niche and may be more sensitive to environmental change, tend to have more restricted and heterogeneous spatial distributions (Brose, 2001; Lyons & Willig, 2002).

From an evolutionary perspective, several hypotheses may be invoked to explain this pattern. For instance, many currently temperate clades appear to have originated in the tropics (Hawkins *et al.*, 2005). Some temperate lineages seem to have diversified massively into the tropics (Jablonski *et al.*, 2006) whilst, in contrast, tropical lineages appear to have difficulties in diversifying and adapting into temperate regions (Hawkins *et al.*, 2006). The lower rates of extinction and higher rates of speciation in the tropics can also explain this diversity pattern (Mittelbach *et al.*, 2007). This higher tropical net diversification (speciation minus extinction) rate seems to be a result of the higher seasonal and longer term climatic stability (Haffer, 1969; Dynesius & Jansson, 2000), an area effect (Terborgh, 1973; Rosenzweig, 1995) and the increased strength of biotic interactions and faster speciation (Fischer, 1960; Schemske *et al.*, 2009). For the historical aspect, tropical taxa are generally older allowing them to evolve and to diversify more rapidly (Fischer, 1960; Mittelbach *et al.*, 2007).

Patterns of species richness along elevational gradients have also received considerable attention (e.g. Sanders, 2002; Bachman *et al.*, 2004; Kessler *et al.*, 2005; McCain, 2010; Acharya *et al.*, 2011; Sun *et al.*, 2013). This pattern is often expected to mirror the latitudinal gradient because of the similarity between climatic conditions at higher elevations and higher latitudes (Rahbek, 1995). Habitat structures such as vegetation and shelters, as well as environmental variables such as temperature and

humidity, vary with elevation, making elevational gradient surveys an excellent model system to analyse the role of environmental condition in structuring community assembly.

Unlike the latitudinal gradient, elevational variation occurs at a much smaller spatial scale, at a vastly greater level of natural replication, and presents more variety of patterns. Elevational diversity patterns depend strongly on the studied taxonomic group and the location of the gradient. Three main contrasting patterns have been documented (McCain & Grytnes, 2010): (1) a decrease of species diversity towards high elevation, as shown for example, in woody phanerogams (Gentry, 1988), herpetofauna of leaf litter (Scott, 1976; Fauth *et al.*, 1989), and anuran amphibians (Duellman, 1999), (2) a hump-shaped relationship between species richness and elevation as shown for birds (Terborgh, 1977), insects (McCoy, 1990; Yu *et al.*, 2013), epiphytic vascular plant (Sugden & Robins, 1979; Gentry & Dodson, 1987; Kluge & Kessler, 2006), or bryophytes (Gradstein & Pócs, 1989; Wolf, 1994; Ah-Peng *et al.*, 2012, 2014) and (3) an increase of species diversity towards high elevations as shown for bryophytes in North-eastern Peru (Gradstein & Frahm, 1987); and lichens (Sipman, 1989); and (4) more recently a double peak of diversity for ground bryophytes (Sun *et al.*, 2013).

1.2. Feature and functional diversity - beyond species richness

Understanding how biodiversity influences ecosystem functionality is currently one of the central topics of ecological researches (e.g. Hooper *et al.*, 2005; Vaughn, 2010; Flynn *et al.*, 2011; Kluge & Kessler, 2011; Sutton-Grier *et al.*, 2011; Cardinale *et al.*, 2012; Clark *et al.*, 2012; Harrison *et al.*, 2014; Tilman *et al.*, 2014; Liang *et al.*, 2015; Turnbull *et al.*, 2016). Linking biodiversity to ecosystem functioning is an important tool for understanding the consequences of biodiversity loss (Vaughn, 2010) and for predicting the effects of climate change on ecosystem services. Biodiversity is a response variable that is affected by changes in climatic (rainfall, temperature, etc) and substrate (geology and soils) conditions, and disturbance-recovery processes. It has the potential to influence the rate, magnitude, and direction of ecosystem processes. Furthermore, the influence of biodiversity on ecosystem functioning depends crucially on how species are different from each other in terms of functional traits and evolutionary history (Flynn *et al.*, 2011; Clark *et al.*, 2012).

The term biodiversity was formally defined as “*the variability among living organisms from all sources, including, ‘inter alia’, terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity*”

within species, between species and of ecosystems” (United Nations Conference on Environment and Development in Rio de Janeiro, 1992). The processes in the evaluation of biodiversity are the observation and characterization of the main units of variation (species and ecosystems), and the quantification of the variability within and between them (taxonomic relatedness) (Bisby *et al.*, 1995; Schwartz *et al.*, 2000; Swingland, 2001; Lavergne *et al.*, 2010; Pavoine & Bonsall, 2011). Ecosystem processes are affected by species functional characteristic, rather than the taxonomic identity (Grime, 1998). Using species richness as a simple measure of biodiversity has less explicit explanatory power if one aims to elucidate the effects of biodiversity on ecosystem function, unless functional attributes of species are considered (Hooper *et al.*, 2005; Cavender-Bares *et al.*, 2009).

1.3. Madagascar – a highly threatened hotspot of biodiversity

Madagascar is the world’s fourth largest island, with an area of ca. 590,000 km², extending 1670 km from 11°57’ S to 25° 32’ S and 560 km from 43°14’ E to 50° 27’ E. It is located entirely in the inter-tropical zone, in the Indian Ocean, off the south-eastern coast of Africa (Figure 1).



Figure 1: Madagascar and the Indian Ocean islands Hotspot of biodiversity (source: https://commons.wikimedia.org/wiki/File%3AMadagascar_and_the_Indian_Ocean_Islands_Hotspot_2005_Print.tif)

1.3.1. Topography and climate

One of the main geographical features of Madagascar is its asymmetrical topography. The eastern slope rises quickly to over 1500 m above sea level within only 100 km. The western slope rises much more slowly, bordering a broad belt of coastal lowlands enclosing two major sedimentary basins (Ganzhorn *et al.*, 2014).

Madagascar's topography plays a key role in shaping its distinct climatic zones. The Madagascan climate exhibits marked seasonality and sharp climatic gradients because of the expanse of latitudes covered by the island and its mountainous nature. The north of Madagascar experiences an equatorial climate with warm, dry, windy winters and steamy summers swept by tropical thunderstorms (Jury, 2003). The south is dry and subtropical. The central highland plateau of Madagascar rises to at least 1000 m. It comprises three major massifs, reaching to 2900 m in the north, 2650 m in the centre and 2658 m in the south of the island (Guillaumet *et al.*, 2008). The eastern mountains capture the humid trade winds blowing from the east. Eastern trade winds cause high rainfall on the eastern slopes of these mountain chains, and a steep rainfall gradient from the tropical humid northeast and east to the sub-arid southwest of the island (Vences *et al.*, 2009). This is called orographic rainfall. Thus, the coastal east is rainy year-round as trade winds are forced to rise up the escarpment along a north-south extent of more than 1000 km.

The variations in climatic conditions are mainly caused by interactions among i) the dry trade-winds from the south-east generated by the Mascarene anti-cyclone during winter (May-September), ii) the monsoon-wind from the north-west generated by the equatorial low-pressure systems during summer (December-March), iii) the geographic location and relief, and iv) the tropical ocean (Jury, 2003).

These abiotic conditions have shaped Madagascar's major biomes grading from tropical humid to sub-arid bioclimatic extremes. The climatic and biotic disparities within Madagascar led to the subdivision of the island into sharp subunits corresponding broadly to its major biomes, defined by either bioclimatic factors or by vegetation and elevation, or by faunal composition.

Cornet (1974) described five main bioclimatic regions for Madagascar namely, the eastern rainforests, western dry deciduous forests and southwestern sub-arid spiny forests, all separated by a mosaic of woodlands and grasslands (Figure 2) (Moat and Smith, 2007; Bond *et al.*, 2008). The bioclimatic system of Cornet explains Madagascar's sharp bioclimatic borders.

As one of the top biodiversity hotspots on earth, Madagascar has exceptional plant species richness and concentrations of endemic species, but it has lost more than 70% of its original primary vegetation. Due to its high levels of habitat loss and degradation, Madagascar is among the highest priority areas in the world for biodiversity conservation (Myers *et al.*, 2000; Mittermeier *et al.*, 2005).

1.3.2. Flora and vegetation

Madagascar is covered by a rich array of vegetation types (Ingram & Dawson, 2005). Du Puy & Moat (1996) classify the primary vegetation of Madagascar into two formations (Figure 3) - evergreen (East and Center) and deciduous. The former was subdivided into Coastal forest (East), Evergreen low elevations humid forest (0-800 m), Evergreen mid elevation humid forest (800-1800 m), Lower montane evergreen humid forest, Mountain shrubland (*Philippia*) (>1800 m), Evergreen sclerophyllous (*Uapaca*) woodland (800-2000 m), and Marshland (0-800 m). The deciduous formation (West and South) was subdivided into Coastal forest (West), Western deciduous seasonally dry forest (0-800 m), Southern deciduous dry forest, and Shrubland (0-300 m).

1.3.3. Species richness and endemism

Due to its exceptionally rich and unique biodiversity, Madagascar has frequently been described as a living laboratory of evolution, and a model of species diversification (Goodman & Benstead, 2005; Vences *et al.*, 2009; Callmander *et al.*, 2011). Madagascar's endemic species have thrived and diversified in isolation for over 100 million years (Ganzhorn *et al.*, 2001; Goodman & Benstead, 2005). The flora of Madagascar has been estimated at 12,364 species (Callmander *et al.*, 2011; Marline *et al.*, 2012). About 85% of the vascular plants (Goodman & Benstead, 2005; Callmander *et al.*, 2011) and 90% of the fauna are endemic to the island (Goodman & Benstead, 2005). Specifically, for its fauna, 100% of amphibians, 98% of land mammals, 92% of reptiles, and 44% of bird species are endemic. For vascular plants, more than 80% of flowering plants, 45% of ferns and 85.71% of gymnosperms are endemic (Rakotondrainibe, 2003; Vences *et al.*, 2009; Callmander *et al.*, 2011). For its flora, this high level of endemism is found not only at species level but also for genera and family level: five families (2%) and 20% of plant genera are endemic to the island.

Bioclimate14

(after Cornet, 1974)

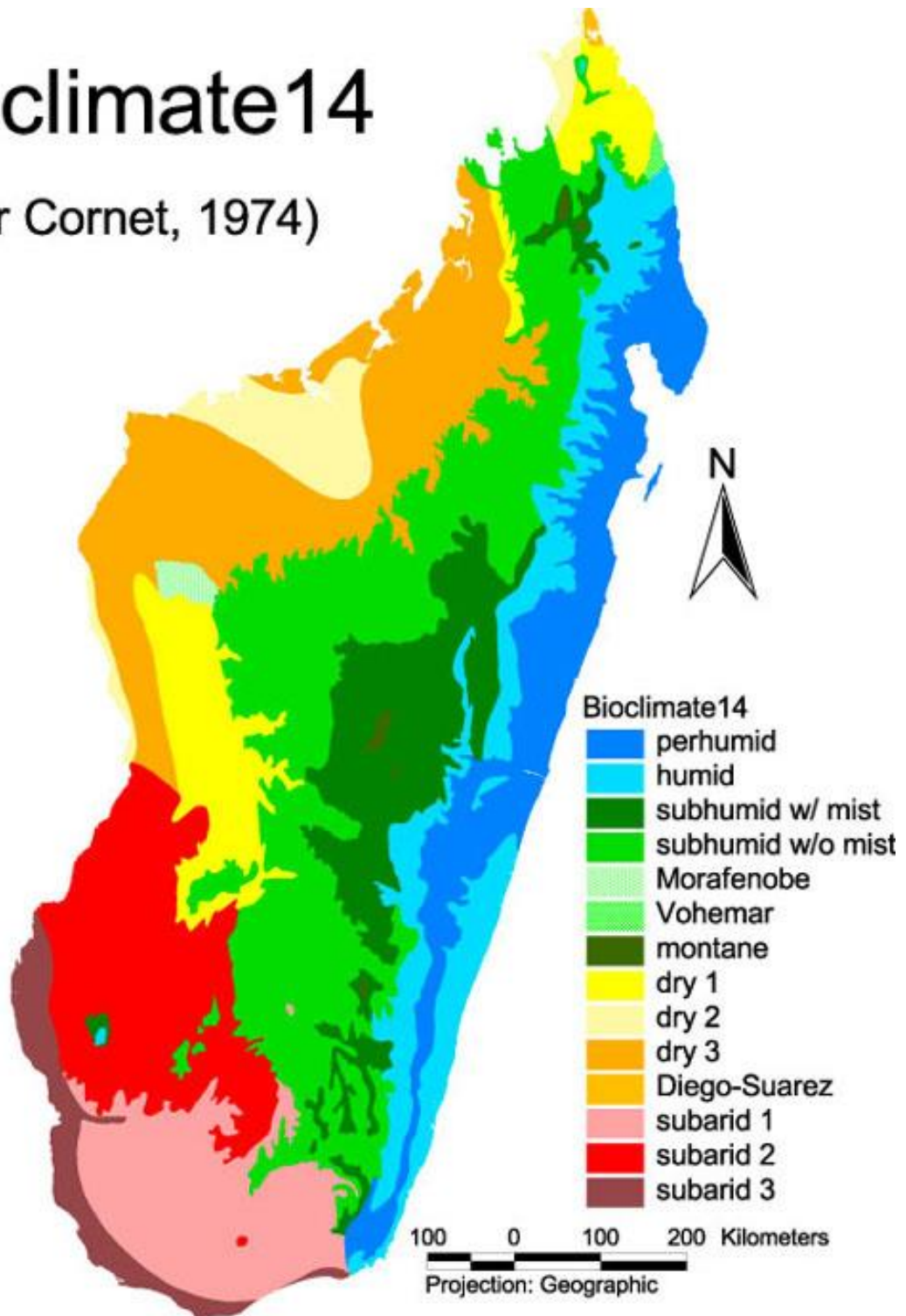


Figure 2: Bioclimatic regions of Madagascar (Cornet, 1974)

Madagascar

Remaining Primary Vegetation

David Du Puy & Justin Moat

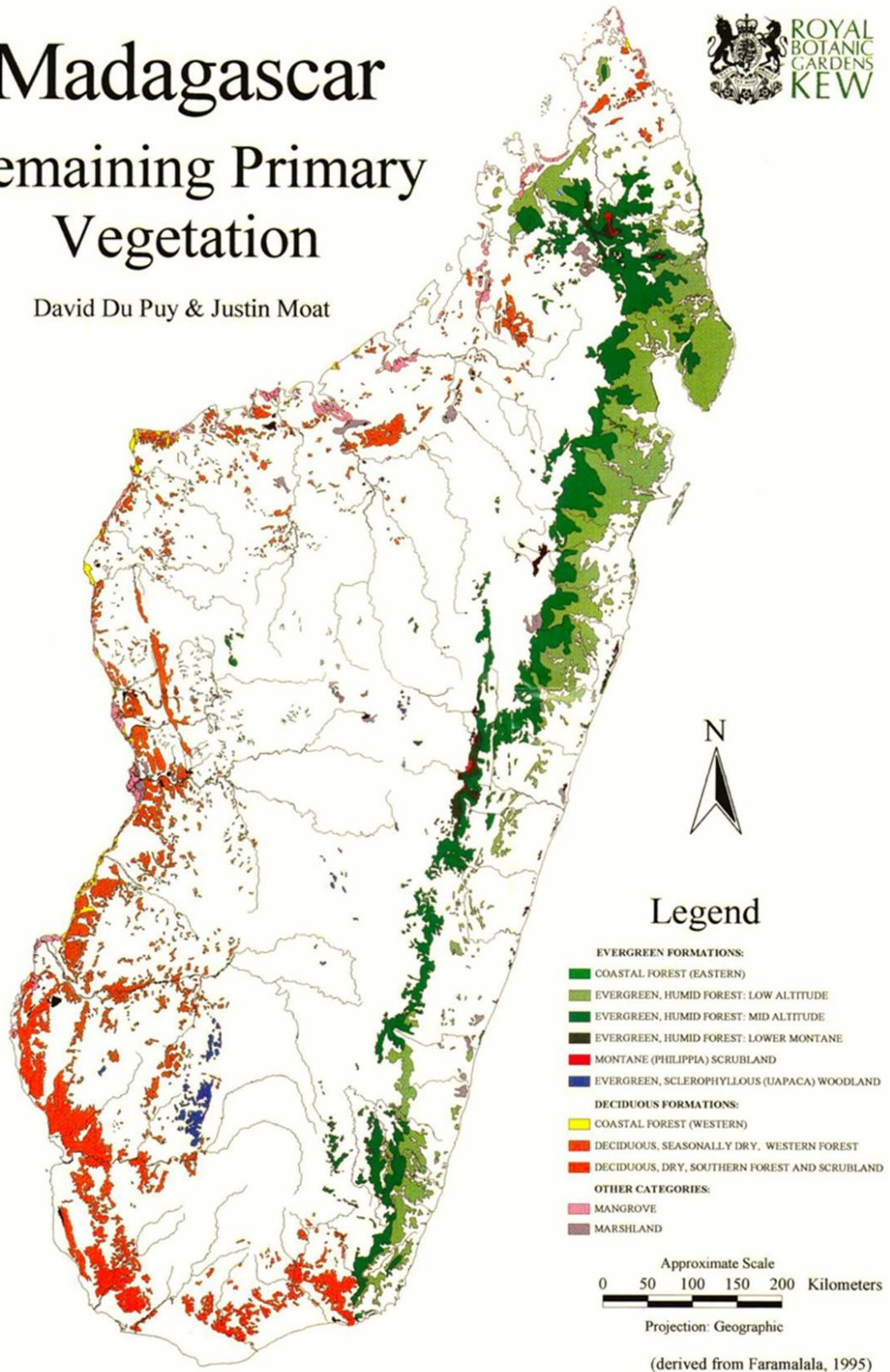


Figure 3: Vegetation of Madagascar (Du Puy & Moat, 1996)

1.3.4. Threats and conservation

Madagascar's exceptionally rich and highly endemic biota (Goodman & Benstead, 2005) is severely threatened (Ganzhorn *et al.*, 2001). It is estimated that about 90% of the island's unique biota is forest-dwelling (Dufils, 2003), but only 10% of the original forest cover that existed before human colonization c. 2,000 years ago remains (Goodman & Benstead, 2005). With forests, as with other habitats, loss of area is one of the biggest threats to biodiversity and is the leading cause of species extinction. Tropical deforestation accelerated in the 1980's (Reid, 1992), with many tropical rain forests rapidly cleared, mainly for agriculture or mining (Laurance *et al.*, 2009). This is also the case for rainforest in Madagascar. Slash and burn (locally called *tavy*) an ancestral agricultural activity consisting of cutting and burning native forest to create crop field, especially rice plantations, is one of the main causes of deforestation in Madagascar (Ingram & Dawson, 2005). The high value of Malagasy hardwoods, especially ebony and rosewood, makes illegal logging a significant problem especially in the eastern rainforests. The other major causes of deforestation include intensive fuelwood and charcoal production in the south-west, and elsewhere include, *inter alia*, commercial logging, plantation farming, road clearance and urban development.

1.4. Bryophytes, a poorly known group in Madagascar

1.4.1. Bryophytes: early land plants

Bryophytes are non-vascular plants and comprise the earliest diverging lineages of land plants (>400 Mya). Bryophytes comprise liverworts (Marchantiophyta), mosses (Bryophyta) and hornworts (Anthocerotophyta). They are, in terms of species numbers, habitat diversification and geographical distribution on all continents, the most successful group of plants other than angiosperms (Schofield & Crum, 1972; Shaw, 2001). Bryophytes dispersal is by small wind-dispersed spores, which can potentially be distributed over very large distances (Van Zanten & Pócs, 1981). On a local scale, the predominant means of dispersal of bryophytes may be by gametophyte fragments or specialized asexual reproductive structures but most long-distance dispersal is presumably accomplished by spores (Miles & Longton, 1992).

There are more than 16,000 species of bryophytes in the tropics (Slack, 2011) and approximately 23,000 described species worldwide. . They exhibit a high species richness

and endemism rate for Madagascar, which count 1144 species and infraspecific taxa: 751 mosses, 390 liverworts and 3 hornworts (Marline *et al.*, 2012).

Bryophytes are poikilohydric (Pardow *et al.*, 2012; Pardow & Lakatos, 2013), i.e. their hydration status depends to a great extent on the water content of their surrounding environment. Many species have the ability to desiccate completely as the surrounding environment dries out but to then rapidly resume photosynthesis and growth upon rewetting (Proctor, 2000; Proctor *et al.*, 2007; Pardow & Lakatos, 2013). They lack a root system, but water and nutrients are taken up over the whole surface of the plant. This can explain the high sensitivity of bryophyte species to air and water pollution (Govindaparyi *et al.*, 2010). Therefore, bryophytes can be used as bio-indicators of air and water pollution (Rao, 1982; Ah-Peng & Rausch De Traubenberg, 2004; Rausch De Traubenberg & Ah-Peng, 2004). They also have significant nutrient retention capability (Clark *et al.*, 2005), affecting nutrient cycling within forests (Coxson, 1991; Curtis *et al.*, 2005).

Bryophytes also exhibit functional diversity (e.g. drought tolerance, water retention, etc) allowing them to survive in a wide range of climates and habitats. They can be particularly sensitive to climatic variation and are appropriate candidates for detecting the biological effects of climate change (Gignac, 2001; Bergamini *et al.*, 2009). Bryophytes can be utilised to reflect long-term micro-climatological changes (Zartman & Pharo, 2007), to understand the evolution of ecosystems and to better manage resources from a biodiversity perspective.

Bryophytes can be important component of forest biomass, especially in tropical montane systems (Pócs, 1982; Holz & Gradstein, 2005; Gehrig-Downie *et al.*, 2011). In some areas, they are usually the first plants to grow on open ground, and there play important roles in reducing soil erosion and holding water and even in soil fertility (Hallingbäck & Hodgetts, 2000; Turetsky *et al.*, 2008, 2010). Bryophytes have a particularly high surface area; this feature, combined with their high water retention capacity, hygroscopic capacity as measured relative to dry weight, and insatiable affinity for capturing water from mist (Ah-Peng *et al.*, 2017), contribute to bryophytes playing a significant role in mist forests (Muchura *et al.*, 2014). Furthermore, bryophytes vegetation shelter community of numerous small invertebrates as well as plants such as orchids and ferns (Gradstein, 1992).

1.4.2. Epiphytic bryophytes in tropical mountain rainforests

Tropical rain forests are well known for supporting a great diversity of flora and fauna. Because of their structural complexity, and habitat heterogeneity, tropical montane and lowland rain forests are home to many bryophytes, holding 25-30% of the world's known species (Gradstein & Pócs, 1989). In fact, Gradstein & Pócs (1989) have stated that the tropical rain forests, including the tropical montane forest, possibly hold more bryophyte species and higher epiphytic bryophyte biomass than any other major ecosystems of the world (Pócs, 1980; Wolf, 1993). Studies on epiphytic bryophytes in tropical montane cloud forests have provided evidence of their important role in rainfall interception (Pócs, 1974, 1980; Veneklaas *et al.*, 1990) and in cloud water interception (Ah-Peng *et al.*, 2017).

Initial research suggested that in a tropical rainforest, bryophytes increase in abundance and species richness along an elevational gradient (e.g. Gradstein & Pócs, 1989; Frahm, 1990; Frahm & Gradstein, 1991). According to Cornelissen & Gradstein (1990), the lowland tropical rain forest might have a much richer bryophyte flora than previously believed when the canopy is properly inventoried. Pócs (1982) and Richards (1984) have implied that as far as tropical forests and bryophytes are concerned, the ambient humidity, total annual rainfall, and length of dry period are much more important parameters than the prevailing temperature.

Taxonomically, about 90% of the bryophytes of tropical rain forests belong to only 15 families: the moss families Calymperaceae, Dicranaceae, Fissidentaceae, Hookeriaceae, Hypnaceae, Meteoriaceae, Neckeraceae, Orthotrichaceae, Pterobryaceae and Sematophyllaceae; and the liverwort families Frullaniaceae, Lejeuneaceae, Lepidoziaceae, Plagiochilaceae and Radulaceae (Gradstein & Pócs, 1989).

Surveys of biodiversity along elevational gradients in most of the high summits of Madagascar have been undertaken by Goodman and various associates (e.g. Goodman, 1996, 2000a). However, only one survey conducted in the Manongarivo Special Reserve included bryophytes, this consisting only of a floristic inventory (Pócs & Geissler, 2002). Most of these studies were focused on describing the pattern of species diversity and distribution. To date, no studies have been done to understand the patterns of distribution and diversity of bryophytes in Madagascar mainly due to the lack of specialists and taxonomical literature, especially for this biogeographical area.

1.5. Objectives, research questions and thesis outline

The overall motivation for this thesis can be clustered into two main objectives: (1) to understand the regional and global context of the bryophytes of Madagascar through a historical, floristic and phytogeographic synthesis; and (2) to understand factors affecting diversity, distribution and assemblage of epiphytic bryophyte communities along an elevational gradient, toward a better understanding of the role of biodiversity in ecosystem functioning. This study presents the first comprehensive taxic and ecological survey of bryophytes in any Madagascan system.

Given that the bryoflora of Madagascar is the most poorly documented component of the Malagasy vegetation, this thesis begins with a mostly literature based overview of the bryological exploration of the island and an assessment of existing herbarium collections for Madagascar (Chapter 2). Since the publication of the first checklist of the bryophytes of Madagascar (Marline *et al.*, 2012), changes have been made in the nomenclature of different families and many species have been newly recorded. However, data on bryophytes species geographical distribution are seldom available for phytogeographic studies. An overview of diversity and endemism of the bryophytes of Madagascar, their phytogeographic patterns and their affinities with neighbouring islands are presented in Chapter 3.

Madagascar, because of its evolutionary origin and geological history, is an ideal region in which to study pattern and process in species diversification and distribution (Vences *et al.*, 2009). Describing spatial variation in species richness and understanding its links to ecological mechanisms are complementary approaches for explaining geographical patterns of richness. The influence of elevational variation on the diversity and distribution of species is notable for an increase in research. The study of elevational gradients holds enormous potential for understanding the factors underlying global diversity. In Chapter 4, I examine the pattern of species richness and range-size distribution of epiphytic bryophytes along an elevational gradient on Marojejy National Park, in North-east Madagascar. These data are then utilised to evaluate how environmental variables and geometric constraints affect the observed richness pattern.

Assessing the spatial variation in species composition of different communities is a key feature in understanding the processes that generate and maintain biodiversity (Legendre & De Cáceres, 2013). The partitioning of diversity into hierarchical scale-related components is one interesting approach to understanding the organisation of diversity. It is a promising approach to quantitatively defining the overall net biodiversity

from hierarchically scaled studies (Crist *et al.*, 2003; Gering *et al.*, 2003) and is a useful method in studies of conservation biology and restoration (Lande, 1996). Chapter 5 deals with the additive partitioning of the overall diversity and the partitioning of beta-diversity. The aim is to describe the variation in species composition between sites and to elucidate why different species occur in different communities. Furthermore, I document how the two components of beta-diversity (turnover and nestedness) are influenced by variation in elevation.

To better understand species interaction and community assembly, a trait-based approach assessing community diversity might be as important as, and/or more meaningful than other community ecology approaches (e.g. species richness or species composition) (McGill *et al.*, 2006; Cadotte *et al.*, 2011). Depending on their exact nature, traits are linked to species ecological strategies and directly influence species interactions (Steneck & Dethier, 1994; Lavorel & Garnier, 2002; Kleyer *et al.*, 2012). The importance of traits along elevational gradients has been investigated within single taxa of different population (Berner *et al.*, 2004) and on a community assemblage level (Gaston *et al.*, 2008; Leingärtner *et al.*, 2014). What is missing is a thorough documentation of changes in community structure, and associated adaptive trait patterns, along environmental gradients. In Chapter 6, I use a trait-based approach to assess the relationship between bryophyte species functional diversity and community assembly. I evaluate how bryophyte species functionally interact with their abiotic and biotic environments and how habitat filtering and niche differentiation influence bryophyte assemblages along an elevational gradient.

CHAPTER 2

An historical overview of bryology in Madagascar

2. An historical overview of bryology in Madagascar

2.1. Introduction

The fauna and flora of Madagascar have intrigued natural historians for centuries and continue to attract great interest. Etienne de Flancourt (1607-1620) begins his “Natural History” chapter in *The History of the Island of Madagascar* with a statement praising the great number of animals, including birds and fish, as well as plant rarities, on the island. Dr. Philibert Commerçon, a French botanist, wrote “Quel admirable pays que Madagascar!” (extracted from his letter to Lalande in 1770). He posited, “*C’est la véritable terre de promission pour les naturalistes. C’est là que la Nature semble s’y être retirée comme dans un sanctuaire particulier, pour y travailler sur d’autres modèles que ceux auxquels elle s’est asservie dans d’autres contrées*” (Rozier, 1775).

The number of biologists working in Madagascar has increased exponentially over the past few decades and information on the biota of the island has expanded proportionately. Many studies have been carried out on both the fauna and flora of the island and these have been well synthesized and illustrated in the recent, massive, multi-authored tome *The Natural History of Madagascar* (edited by Goodman & Benstead 2004).

Whilst the flora of Madagascar has received significant attention over the last four centuries, certain groups such as bryophytes, although ecologically critical, have received little attention. Although bryophytes represent nine percent of the flora of Madagascar and four percent of the endemic species (Marline *et al.*, 2012), they are the most poorly documented component of the Madagascan vegetation. Most studies of this group to date have focused mainly on taxonomy and floristic inventory. Despite many bryological explorations, inventory and description, knowledge on the bryophyte flora of Madagascar is far from complete.

In this chapter, I provide an overview of the history of bryophyte collectors and expeditions in Madagascar, the state of bryophyte collections in the National Herbarium in Antananarivo and ongoing research on the bryophytes of the region. This historical overview is based on literature review and herbarium collections, mainly from the National Herbarium of Madagascar (TAN) and the National Museum of Natural History (PC) in France. Throughout this chapter, herbarium abbreviations follow Thiers (2010).

2.2. Bryophyte collectors and expeditions

Since the arrival of Europeans in Madagascar in 1500, scientists, initially mainly French, have become increasingly interested in exploring the island and have often noted its unique biological diversity. However, it was only at the end of the 18th century that collectors began to explore and collect bryophytes, with French soldiers, botanists and missionaries playing a key role and generally among the first to collect bryophytes on the island. Most of their collections are located in various international herbaria with few of them published in the literature. Biographical data for botanical collectors in Madagascar are reported in Dorr (1997).

Three phases can be differentiated in the history of bryological expeditions to Madagascar. They can be linked to the political history of Madagascar: the Malagasy Monarchy, the French Colonial era, and the post-independence phase since 1960.

Phase 1: The Malagasy Monarchy (1810-1897)

Europeans, mostly missionaries, began to arrive in Madagascar during the reign of King Radama I (1810-1828), the second king of Madagascar. From 1883, the French invaded Madagascar, first taking possession of Diego Suarez in the northern part of the island, (Randrianja & Ellis, 2009). During the reign of Queen Ranaivalona II (1868-1883), missionaries returned to Madagascar after being expelled from the island by the previous queen. Catholic and protestant missionaries subsequently arrived in numbers to build churches and schools.

Bryophyte collections from this period are predominantly from the north of Madagascar. The main collectors, mainly French botanists, soldiers, missionaries and doctors, made important bryophyte collections. Reverent Martinius Borgen, a Norwegian Lutheran missionary, collected mosses mainly between 1868 and 1877. Marie Edouard Auguste, a sailor and amateur malacologist, collected in 1879. Arbogast, a French priest of Sainte Marie Island, collected in 1890 and 1891. The friar Perrot, a Mauritian, collected from 1890 to 1897. A key feature of this period was the visit of two famous French botanists, Auguste Pervillé and Louis-Hyacinthe Boivin, who left a significant mark in the history of biological exploration in Madagascar, and many species are named after them.

Pervillé (-c. 1868.), a botanist and explorer from the National Museum of Natural History in Paris, was the first to collect bryophytes in Madagascar. He spent several years in the Indian Ocean and made collections from the Seychelles, La Réunion, and Mauritius. According to his letter dated 24 June 1841, to Mr. Brongniart, a Professor and

administrator at the National Museum of Natural History, Paris, he collected vascular plants and bryophytes in Nosy Be and Ampasindava in the North-West of Madagascar. His collections housed in PC date from 1837 to 1841. In total, he collected 800 plant species from Madagascar and the Seychelles, including seven species of *Syrrhopodon*, four of *Taxithelium* and two of *Trematodon*. He collected a further 265 specimens in the North-West of Madagascar and Nosy-Be, but the dates of collection are unknown for most specimens. The species *Dicranella pervilleana* Besch. is named after him.

Louis-Hyacinthe Boivin (1808-1852), a botanist and explorer, was commissioned by the French National Museum of Natural History to serve as a botanical expert on the Oise Expedition in 1846 (Dorr, 1997), which aimed at exploring the East Coast of Africa, the Comoros and Mascarenes, and Madagascar (1846-1852). During this period, he collected around 1000 bryophyte specimens in Madagascar. With Alphonse Charles Joseph Bernier they visited the island of Nosy-Be, then the north-eastern coastal region (Baie d'Antsiranana, Baie de Rigny, Port Lewen and Vohémar) and later headed south to Île Sainte-Marie (Phillipson & Callmänder, 2013). He revisited these localities alone and started to collect mosses. In 1849, he collected two specimens of *Leucoloma sanctaemariae* Besch. from the Île Saint-Marie. In 1850, he made 7 collections of *Trichosteleum* from Saint Marie and the species *Taxithelium kerianum* Broth. from Nosy Be. In 1851, he explored the forest of Lokobe (Nosy Be) and collected 200 samples representing 56 genera and 104 species of mosses and liverworts. Boivin was not a bryological specialist but sent his specimens to bryologists such as Stephani (Botanical Garden of Geneva), who also described a species in his honour, *Plagiochila boivinii* Steph. His bryophyte collections are housed in PC.

Phase 2: The French Colonial Period (1897 - 1960)

The second phase of exploration took place during the period of French colonisation. This phase is characterized by intensive biological exploration of Madagascar. However, most explorations on the flora were mostly focused on the vascular plants and the study of the vegetation of Madagascar. Approximately 40 bryophyte collectors, mainly French botanists, ethnobotanists, missionaries and soldiers collected in Madagascar during this period. This resulted in the discovery of more than half of the presently known species and the description of many putative endemics. Bryophyte collections from this period are mainly held at PC. The bryophyte collectors who made significant collections of bryophytes and vascular plants, numerically and taxonomically, are:

Pierre Louis Besson (1855-1941), a physician, administrator and naval doctor from France, collected 441 specimens of mosses and liverworts from Eastern Madagascar (the forests between Mananjary and Fianarantsoa), and South-eastern Madagascar (pays des Antanala, Sandravonona and Ranomafana).

Paul Camboué (1849-1929), a French missionary (1888 to 1907), collected 402 specimens comprising 191 species of mosses and 11 of liverworts around Antananarivo, the Analamazaotra forest, Arivonimamo and Ambatovory.

Raymond Decary (1891-1973), an administrator, naturalist and ethnographer, collected 254 specimens in the Massif of Ankarafantsika (South-east), and near Ambatofinandrahana (Northern Madagascar).

Perrier de La Bâthie (1873-1958), collected vascular plants and bryophytes. He authored "*La Végétation Malgache*" (1921), the first published classification of the vegetation of Madagascar, and edited the "*Catalogue des Plantes de Madagascar*" (Perrier de la Bâthie, 1934). He collected bryophytes between 1904 and 1927 around Antananarivo, Mangoro, Ambalavao, Fianarantsoa, and in the North between Nosy Be and Analalava. He also collected in many of the high mountains of the country, including Andringitra, Ankaratra, Tsaratanana and Tsiafajavona, as well as in the Montagne d'Ambre, Andasibe-Analaazaotra, the Manongarivo forest and Isalo. He collected 684 bryophyte specimens, mostly mosses.

Henri Humbert (1887-1967), was another French botanist interested in the classification of the vegetation of Madagascar. He explored the flora of the central mountains of Madagascar and the Imerina region in 1912, the mountains of the south-eastern part in 1928, and the western and south-eastern parts of the island during 1933-1934. During those expeditions, he collected a few specimens of bryophytes. It was only during his 7th expedition that he visited Marojejy, north-eastern Madagascar, becoming the first explorer of bryophytes from that region. He collected 86 samples of bryophytes in this area.

Phase 3: The period of Independent Madagascar (1960 to present)

After Madagascar achieved independence from French colonisation in 1960, there was an increasing interest in the bryophytes of the island, enormously raising the recorded species numbers as specialists in bryology started to explore the region.

Onraedt Frere Maurice, a Belgian clergyman and cryptogamist, was the first specialist bryologist to collect in Madagascar (as well as the Mascarenes and the

Seychelles). He collected in Madagascar in January 1970, August 1971 and March 1974. More recently, Georges Alexis Cremers, a Belgian botanist and agricultural engineer who worked for ORSTOM Madagascar made collections from 1970 to 1975. Pierre Paul Marie Tixier, a French bryologist from the National Herbarium of Natural History in Paris, and Tamas Pócs, a bryologist from Hungary are other bryologists who made important collections, inventories, new descriptions and important taxonomical reviews on the bryophytes of Madagascar.

This phase is also characterised by a succession of bryological expeditions and the most recent ecological studies on the bryophytes of the island. The first major bryological expedition was a multidisciplinary inventory conducted on the north-eastern slopes of the Manongarivo massif (1998-1999). The research group included specialists in the fields of vascular plants, bryophytes, invertebrates, birds, mammals, reptiles and amphibians. This was the first study that combined bryophytes with an inventory of fauna and vascular plants. The bryophyte team comprised Tamas Pócs, Patricia Geissler and András Szabó. Bryophytes collected in the Special Reserve of Manongarivo during this research were reported by Pócs & Geissler (2002). From this expedition, 19 taxa were reported as new to Madagascar and four for the whole of Africa. Samples are mainly held at G with duplicates deposited in TAN and EGR.

The Missouri Botanical Garden (MBG) team in Madagascar has also conducted a few bryological inventories. Most collections are deposited at TAN and MO. More recently, a bryological field trip, led by Roger Lala Andriamirisoa (MBG) and Catherine Reeb (University of Paris VI), was conducted in the following areas: Vohimana Reserve (2006-2012), Vohibola Reserve and Makirovana forest (2010), Makay forest (2011), Maromizaha forest (2012) and Zahamana forest (2013). These field trips were conducted within the framework of a research project on the taxonomy of thalloid liverwort taxa in Africa by the Missouri Botanical Garden Madagascar.

In November 2009, a bryological expedition, BRYOLAT, was conducted in Marojejy National Park. Its main aim was to study the structure of bryophyte assemblages along an elevational gradient. The team included eight bryologists from Madagascar (Andriamirisoa Lala Roger & Lova Marline), South Africa (Terry Hedderson & Nicholas Wilding), Malaysia (Min Chuah Petiot), and France (Jacques Bardat & Claudine Ah-Peng). The sorting out, identification and analyses of these specimens are still in progress. Identifications to date have yielded 39 new records for the island; these are detailed in

[Appendix 2](#). Duplicates of each floristic sample are deposited at TAN. Results from this expedition are partly described in this thesis.

In 2015, a group of bryologists and lichenologists conducted an expedition to collect floristic samples of bryophytes and lichens in Marojejy National Park (north-east), Ankarana National Park (north-west) and Montagne d'Ambre National Park (north). The team included Vololotahina Razafindrahaja and Roger Lala Andriamiarisoa (Madagascar), Damien Ertz (Belgium), Eberhard Fischer (Germany), Bernard Goffinet (United States) and Emmanuel Sérusiaux (France).

2.3. Bryophyte collections in the National Herbarium of Madagascar (TAN)

Madagascan bryophytes specimens have largely been distributed to various herbaria outside the country. The oldest collections of Malagasy bryophytes are hosted at PC in Paris, which holds 4,888 bryophyte samples. The national herbarium (TAN) houses around 1,200 specimens of bryophytes, excluding the latest collection from the BRYOLAT expedition. About 60% of the samples (738) have a complete identification to species rank. An additional 333 specimens are identified to genus and 75 are still without any name ([Figure 4](#)). The few historical samples present in TAN were mainly collected by Bosser, a French botanist from the French National Museum of Natural History. Most TAN specimens were collected after 1960 and the presence of these samples is probably linked with the fact that collecting permit regulations stipulated that the national herbarium receives a duplicate for each sample collected in the country, with the aim of obtaining reference specimens for students and promoting further studies on the local flora. It is important for the local development of knowledge on the bryoflora of Madagascar that a reference collection of bryophytes is hosted at TAN.

During the compilation of the first checklist of the bryophytes from Madagascar (Marline *et al.*, 2012), many of those collections from TAN were not considered as the names given are doubtful and require taxonomic revision. Presently, the collection is being curated and sorted out according to modern taxonomy.

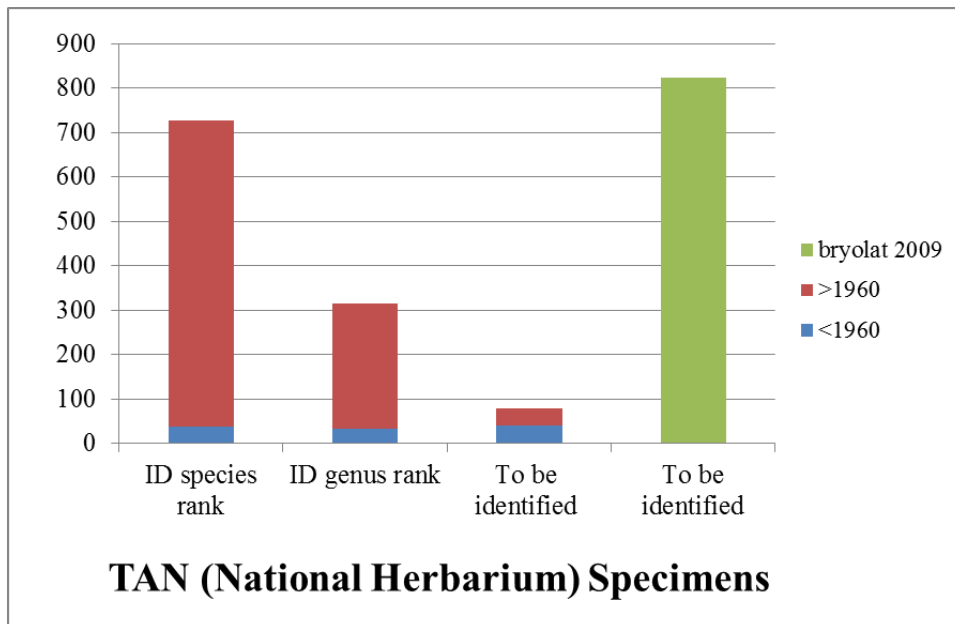


Figure 4: State of identification of Bryophyte specimens in TAN.

2.4. Bibliographic review

Literature regarding the bryophytes of Madagascar is scarce, mostly dating back to the early 20th century, and mainly comprises inventories and species descriptions. Liverworts and mosses were unequally studied. Although liverworts were the first group to be mentioned for the island, mosses received more attention in terms of collections, species descriptions and listings. The bryophytes of Madagascar have generally been studied together with those of its neighbouring islands (e.g. the Mascarenes) or of Sub-Saharan Africa.

The first checklist of liverwort species for Madagascar was published by Lindenberg and Gottsche (1846-1851) in *Species Hepaticarum* (vol. 6-7). This list contains figures and diagnoses but does not include any geographical information. It was in 1874 and 1888 that Hampe (1874) and Wright (1888) produced the first checklists of mosses from Madagascar. Wright's (1888) list of mosses presents the collections made mainly by Borgen (Norwegian Missionary) and Hildebrandt. It also includes Borgen and Borchgrevink's collection described in Hampe (1874) and Boivin's collection newly reported by Bescherelle in 1877 (unpublished). In 1890, Stephani (1890) published *Hepaticae Africanae Novae in Insulis Bourbon, Maurice et Madagascar Lectae* in which he included species diagnoses from the Mascarene Islands and Madagascar. This work was preceded by the work of Spruce on the new bryophyte records from Madagascar (Bescherelle & Spruce, 1889). Pearson (1892a) also produced a list of the species (mostly

mosses) known from the island, including two liverwort families: Frullaniaceae (Pearson, 1891) and Lejeuneaceae (Pearson, 1892b).

A detailed and complete study of the bryoflora of Madagascar, *Prodrome de la Flore Bryologique de Madagascar, des Mascareignes et des Comores* by Renauld (1897), presents a checklist of bryophytes collected in the different Western Indian Ocean islands. It provides species descriptions and geographic distributions for 425 mosses reported for Madagascar, and an enumeration of some liverworts discovered by his correspondents. The *Histoire Physique, Naturelle et Politique de Madagascar*, a 52-volume work published by Grandidier since 1875, is the most synthetic publication on the scientific exploration of Madagascar. Renauld & Cardot (1915) wrote the volume entitled “*Mousses*” in this publication, using the work originally written by Renauld in 1897. It includes species descriptions and geographic distributions, with new records and for the first time, iconographies of taxa.

Other authors, including Paris (1902, 1905) and Levier (1901), have also contributed to our present bryofloristic knowledge of Madagascar. From 1920, Thériot produced her first *Contribution à la flore bryologique de Madagascar* which preceded seven more volumes on the bryoflora of Madagascar extending to 1932, (Thériot, 1920, 1922, 1923, 1924, 1926, 1927, 1930). Thériot’s publications presented a description of bryophytes collected mainly by Perrier de La Bâthie, Potier De La Varde and Decary. Jovet-Ast wrote separately on the liverworts (Jovet-Ast, 1948a) and mosses (Jovet-Ast, 1948b), dealing specifically with their distribution on the island.

More recent enumerations used literature reviews to produce lists of the mosses and liverworts of Madagascar and its neighbouring islands (Grolle & Onraedt, 1974; Crosby *et al.*, 1983). The synthetic works of O’Shea (2006) and Wigginton (2009), who published periodically updated checklists of the bryophytes from Sub-Saharan Africa, including Madagascar, are amongst the most relevant enumerations. Since the publication of the first checklist of the bryophytes of Madagascar more than 120 years ago, the number of species reported for the island has increased considerably: the most recent updates of the checklists of Sub-Saharan African bryophytes report 1112 taxa for Madagascar, comprising 385 liverworts, 2 hornworts and 727 mosses (O’Shea, 2006; Wigginton, 2009). The most recent checklist by Marline *et al.* (2012) reports a total of 1144 species, comprising 751 mosses, 390 liverworts and 3 hornworts ([Appendix 1](#)). A summary presenting published checklists of Madagascan bryophytes is presented in [Table 1](#).

Table 1: List of published checklists of the bryophytes of Madagascar: species recorded by authors.

Publication	Date	Mosses	Liverworts	Hornworts
Marline et al.	2012	751	390	3
Wigginton	2009	-	385	2
O'Shea	2006	727	-	-
Crosby et al.	1983	855	-	-
Jovet-Ast	1948	-	250	-
Renauld & Cardot	1897	425	-	-
Wright	1888	244	-	-

Taxonomical studies including Madagascan representatives of various bryophyte families/genera are fewer. The moss family Leucobryaceae was the first group to be revised for Madagascar and the other Western Indian Ocean island (Cardot, 1904). The genus *Leucoloma* is another genus that has been well studied and revised, first for Madagascar, Comoros and the Mascarenes (Renauld, 1909), and then for Africa and Madagascar (La Farge, 2002a, 2002b, 2002c). The more comprehensive completed revisions include *Breutelia* (De Sloover, 1975); *Leptodontium* (De Sloover, 1987) and the genera *Andreaea*, *Racomitrium*, *Gymnostomiella* and *Thuidium* (De Sloover, 1977). So far, the best documented and thoroughly revised liverwort genera are *Cololejeunea* and *Diplasiolejeunea* (Tixier, 1985) and Vanden Berghen's revision of African representatives of genera including *Frullania*, *Plagiochila*, *Cheilolejeunea* and *Ceratolejeunea* (Vanden Berghen, 1950a, 1950b, 1951, 1981, 1984).

2.5. Conclusion

Knowledge on the bryophytes of Madagascar is far from being complete. To date, most studies have focused on taxonomic and floristic inventories. It appears that collectors were more interested in collecting mosses than liverworts and hornworts. In the past, rainforests have been the main focus of bryologists in Madagascar, attracted by the luxurious bryoflora existing in the mountains.

Most records of bryophytes for Madagascar were collected from areas that are nowadays defined as protected areas and primary forests. The most frequently visited sites are Marojejy National Park, Andasibe-Périnet, Andringitra National Park, Forest of Manjakatempo, Ankaratra Mountain, Ambohitantely Special Reserve, Ranomafana National Park and Anjozorobe National Park. Large parts of the country are still unknown as far as their bryological diversity is concerned. Many areas still need to be inventoried

and this will undoubtedly provide new additions and information concerning the Malagasy bryoflora, which is highly threatened by habitat destruction.

The majority of the Madagascan flora has not been included in either local revisions or those with a broader geographic scope. Therefore, it is difficult to evaluate the status of the many endemics reported from the island. For example, in many of the cases where Madagascan species have been included in regional or global revisions, the numbers of recognised endemics tend to decrease (e.g. So, 2004; Pócs, 2011a, 2011b).

Much work remains to be done to improve knowledge on the bryophyte flora of Madagascar such as updating the bryophyte collection from the national herbarium (TAN) with current taxonomy, and new inventories of intact and unexplored habitats, poorly investigated areas and understudied areas such as the dry forests. Such studies should prove invaluable for verifying many of the old records presented in the checklists of bryophytes from Madagascar. It will undoubtedly reveal many new and biogeographically significant records for the island. The literature review of bryophytes from Madagascar was mainly focused on inventories and species descriptions. Information on bryophyte ecology in Madagascar is scarce and this field requires a great deal of future research. It would be useful if more students and scientists could become involved in future inventories and ecological studies of this diverse plant group in Madagascar.

CHAPTER 3

The Regional and Global Context: floristic and phytogeographic analysis of the bryophyte flora of Madagascar

3. The Regional and Global Context: floristic and phytogeographic analysis of the bryophyte flora of Madagascar

3.1. Introduction

Madagascar, because of its evolutionary origin and geological history, is well known as an ideal region in which to study pattern and process in species diversification and distribution (Vences *et al.*, 2009). Located 400 km east of Africa, Madagascar is the fourth largest island in the world. Together with its neighbouring islands (La Réunion, Mauritius, Rodrigues and the Comoros Archipelago), it is renowned for its exceptionally high levels of endemism and unparalleled habitat diversity (Myers *et al.*, 2000; Mittermeier *et al.*, 2005). These islands are globally amongst the most important priorities for conservation. For instance, 100% of the native Malagasy amphibian and terrestrial mammal species, 92% of reptiles and >90% of plants are endemics (Vences *et al.*, 2009). This is believed to be the consequence of over 100 million years of evolution in relative isolation (Callmander *et al.*, 2011). Some endemic lineages of the island are relicts of the breaking away from, from India 96-65 Mya, Antarctica 130 Mya and Africa 183-158 Mya. Land bridges to Antarctica, and thus connections to South America probably persisted until 90-80 Mya. Many endemic lineages have also resulted from dispersal across the Mozambique Channel of African by founder individuals during the Cenozoic, i.e. from 65.5 Mya to the present (Vences *et al.*, 2009).

Bryophytes are, in terms of species numbers, habitat diversification and geographical distribution on all continents, the most successful group of plants other than angiosperms. They inhabit an astounding diversity of substrates, ranging from littoral to montane zones and from the polar regions to the tropics. Their abilities to survive in a small microenvironment, long after the general climate of the region has deteriorated, make them excellent candidates for phytogeographic studies. In general, bryophyte species have broad geographical ranges that often span more than one continent. This transoceanic disjunction, frequent distribution pattern for bryophytes, reflect repeated intercontinental dispersal, or ancient distributions (Schofield & Crum, 1972; Van Zanten & Pócs, 1981). Study on multiple liverwort genera suggested that their geographic distributions may be explained by continental drift (Vanderpoorten *et al.*, 2010). Regarding the Gondwanan range, few studies on intercontinental distributions show recent origins rather than

Gondwanan ones. For instance, long distance dispersal appears to be responsible for many intercontinental disjunctions previously interpreted as ancient vicariance events (McDaniel & Shaw, 2003, 2005, Heinrichs *et al.*, 2005, 2009).

The bryoflora of Madagascar comprises currently 1144 species and infraspecific taxa: 751 mosses, 390 liverworts and 3 hornworts. In contrast to vascular plants, the bryoflora of Madagascar displays a relatively low level of endemism, with 33.82% of mosses and 18.97% of liverworts confined to the island (Marline *et al.*, 2012). Research on the flora of Madagascar has been long focused on vascular plants rather than groups such as bryophytes. For instance, the *Catalogue of the Vascular Plants of Madagascar* (Madagascar Catalogue, 2013) produced by the Missouri Botanical Garden, analysing and evaluating the current taxonomical status the Madagascan plant genus focuses only on the Madagascan vascular plant.

Since the publication of the first checklist of the bryophytes of Madagascar (Marline *et al.*, 2012), changes have been made in the nomenclature of different families and new species have been discovered. However, data on species geographical distribution are seldom available for phytogeographic study. After years of examination of herbarium specimens (mostly PC and TAN), review of relevant publications and recent collections, it is possible to provide preliminary data on the phytogeographic pattern of the bryoflora of Madagascar.

The aim of this chapter is to (1) update knowledge on the diversity and endemism of the bryoflora of Madagascar, (2) provide preliminary data on the geographic distribution of the bryoflora of Madagascar and (3) elucidate the affinities of the bryoflora of Madagascar with its neighbouring islands.

3.2. Materials and Methods

This general synthesis was compiled from recent literature and supplemented by new bryophyte collections. It is an update on the previous checklist produced by Marline *et al.* (2012).

To analyse the phytogeographic affinities of the Madagascan bryophytes, each taxon was assigned to a group based on its global distribution (Table 2). Distributions were assessed by information available in the literature and in the “Index of Mosses database, W³MOST” from the TROPICOS MOST database. The phytogeographic groups are adapted from those used by Pócs & Geissler (2002).

The bryoflora of Madagascar was compared with the neighbouring islands of

Comoros, Rodrigues, Mauritius and La Réunion, by using floristic data extracted from the work of Wigginton (2009) for liverworts and hornworts, O'Shea (2006) for mosses and Ah-Peng & Bardat (2005) for the bryoflora of La Réunion Island.

The Jaccard's similarity index is used to assess floristic similarity among islands. It summarizes how much two sets of species overlap, using presence and absence data, but ignoring joint absences. It is computed as $S_J = \frac{a}{a+b+c}$, a is the number of species common for two samples 1 and 2, b and c are the number of species unique, respectively to 1 and 2. Thus values near 1 imply high species overlap. Species similarity was computed using the vegan packages in R (Oksanen *et al.*, 2015; R Core Team, 2015).

3.3. Results

3.3.1. Species diversity

The bryoflora of Madagascar is composed of 1188 species and infraspecific taxa. The mosses are the most diverse, comprising 59 families, 187 genera and 760 species and infraspecific taxa. Liverworts comprise 30 families, 86 genera and 425 species and infraspecific taxa. Hornworts are represented by only 2 families, 3 genera and 3 species (Appendix 1, Appendix 2). The majority of the new records are reported from the ecological collection in Marojejy National Park (this study) as well as a few from recent herbarium collections and recent literature.

For mosses, Dicranaceae is the family with the largest number of species (83 species and infraspecific taxa of which 55 belong to the large genus *Leucoloma*), followed by Orthotrichaceae (66 species and infraspecific taxa) and Bryaceae (44 species and infraspecific taxa). The Lejeuneaceae (203 species and infraspecific taxa), followed by Frullaniaceae (38 species and infraspecific taxa) and Plagiochilaceae (21 species and infraspecific taxa) are the richest families for liverworts. Only 37% of moss families and 23% of liverwort families contain more than 10 species. Several families are represented by only one species (Figure 5, Figure 6).

The most species-rich moss genera are *Leucoloma* Brid. (Dicranaceae; 55 species), *Fissidens* Hedw. (Fissidentaceae; 40 species), *Schlotheimia* Brid. (Orthotrichaceae; 31 species), *Bryum* Hedw. (Bryaceae; 26 species), *Macromitrium* Brid. (Orthotrichaceae; 24 species) and *Campylopus* Brid. (Leucobryaceae, 23 species) and *Syrrhopodon* Schwägr. (Calymperaceae; 23 species). The most species-rich liverwort genera are *Cololejeunea*

(Spruce) Schiffner (Lejeuneaceae; 54 species), *Frullania* Raddi (Frullaniaceae; 38 species), *Diplasiolejeunea* (Spruce) Schiffner (Lejeuneaceae) (26 species), *Lejeunea* Lib. (Lejeuneaceae; 22 species) and *Plagiochila* (Dumort.) Dumort. (Plagiochilaceae; 21 species).

From our ecological study in Marojejy National Park, 29 liverworts and 10 moss species were identified as new to the bryoflora of Madagascar. The newly reported liverwort species belong to eight families: Lejeuneaceae (15 species), Lepidoziaceae (4 species), Frullaniaceae (2 species), Lophocoleaceae (2 species), Metzgeriaceae (1 species), Scapaniaceae (1 species) and Cephaloziaceae (1 species). The 15 species belonging to the Lejeuneaceae are distributed in 9 genera. For mosses, the newly reported species belong to 5 families: Leucobryaceae (1 species), Dicranaceae (3 species), Calymperaceae (1 species), Orthotrichaceae (3 species) and Sematophyllaceae (2 species) ([Appendix 2](#)).

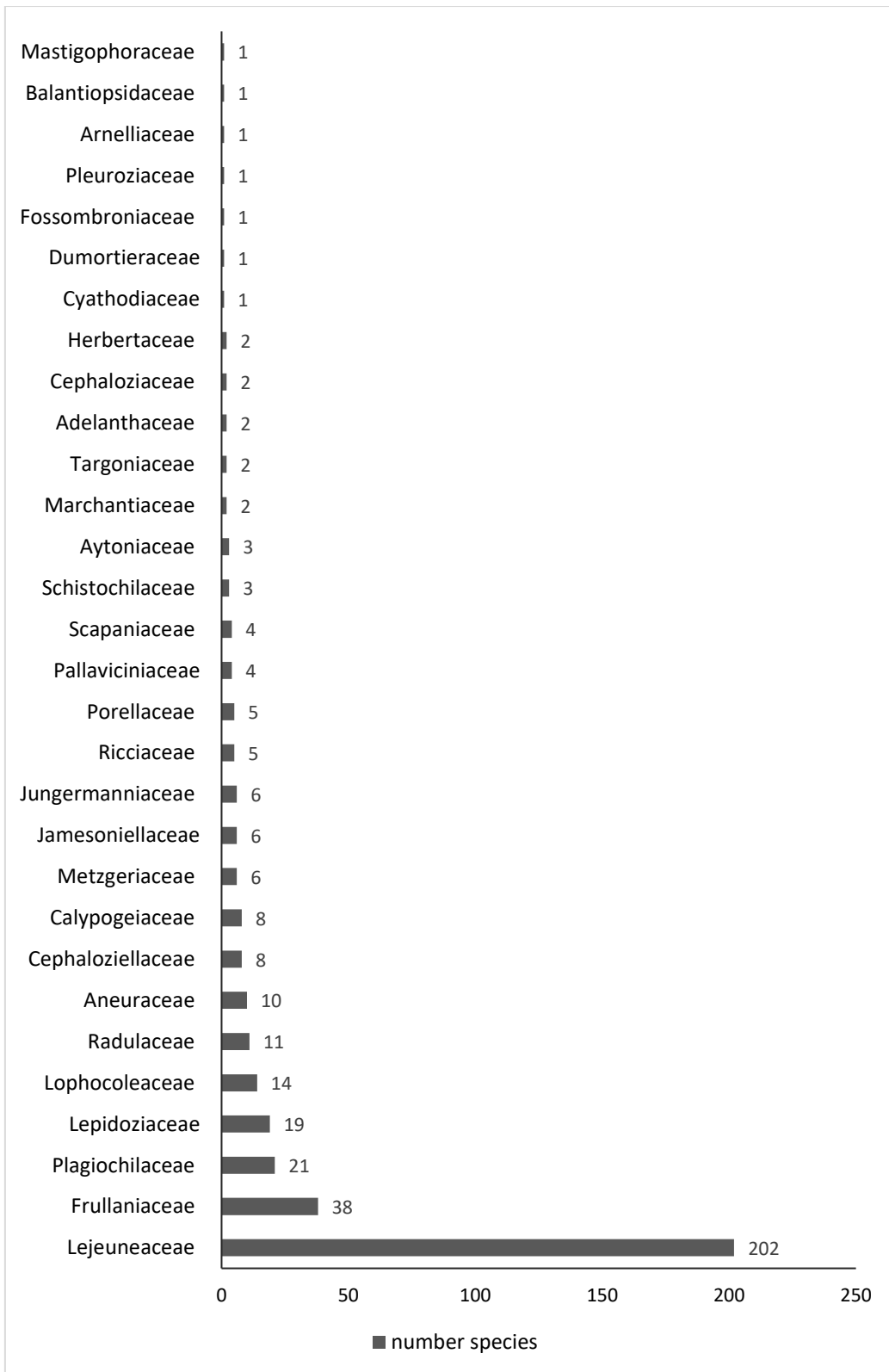


Figure 5: Liverwort species richness by family.

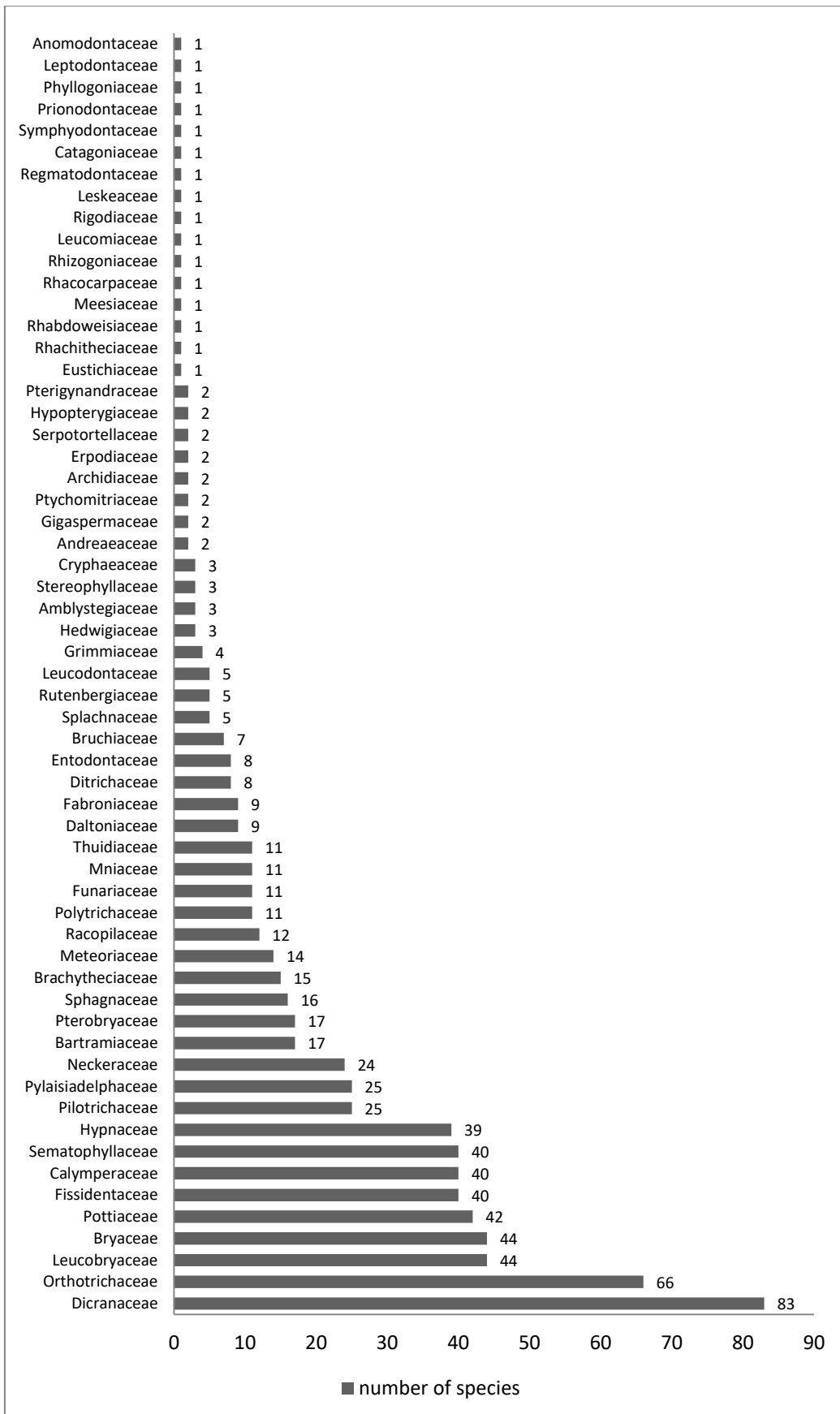


Figure 6: Moss species richness by family.

3.3.2. Species endemism

The bryoflora of Madagascar displays a remarkably high level of endemism with 33.42% of mosses and 17.41% of liverworts restricted to the Island.

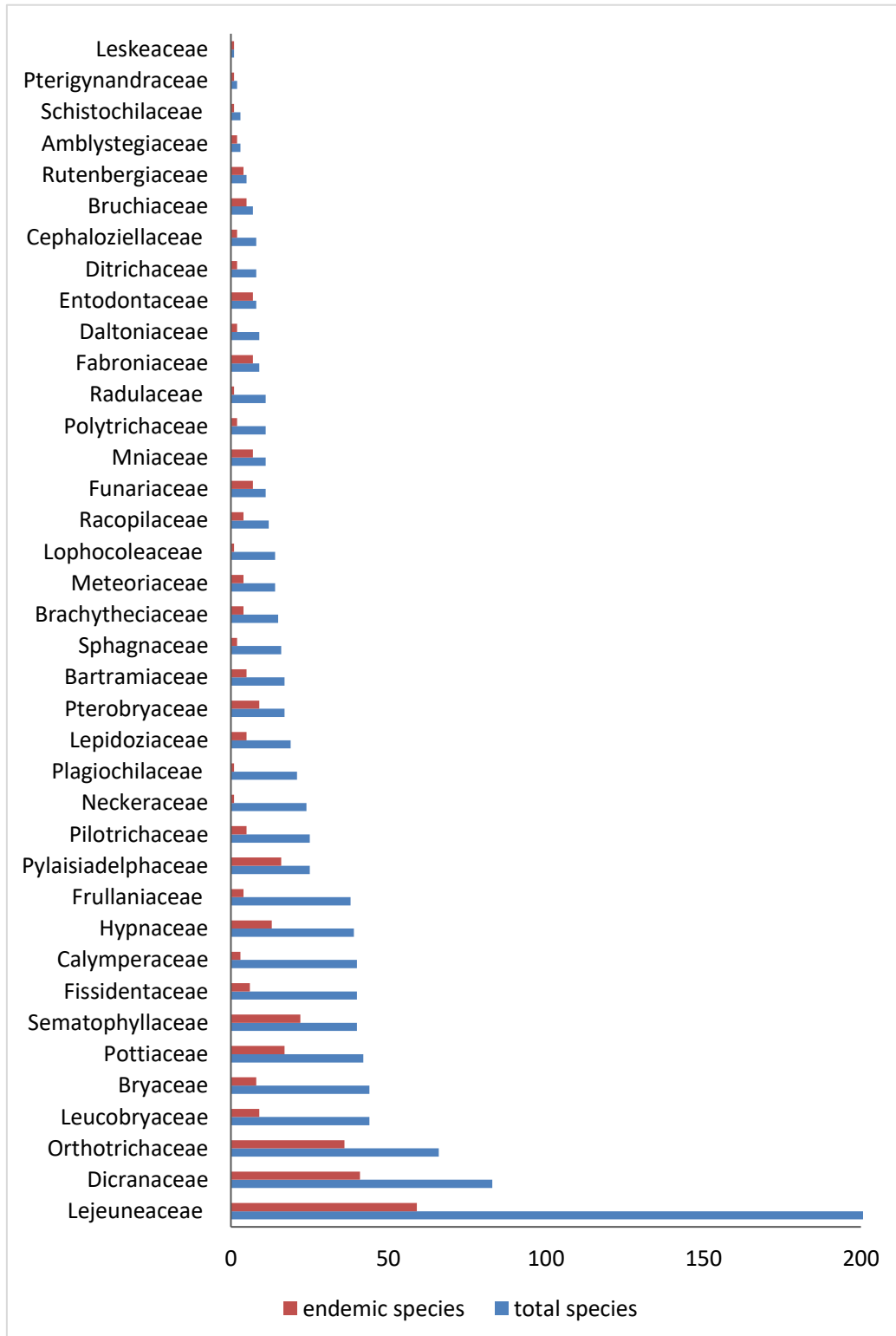


Figure 7: Distribution of endemic species across bryophyte families.

For mosses Dicranaceae have the largest number (41/83) of endemic species, followed by Orthotrichaceae (38/66) and Sematophyllaceae (22/40) (Figure 7). Fifty-nine of the 74 endemic liverwort species recorded on the island belong to the family Lejeuneaceae, of which the most important is the epiphyllous genus *Cololejeunea* (20 of 54) which has radiated throughout Madagascar and the neighbouring islands (Tixier, 1985), and genus *Diplasiolejeunea* (13 of 26). The tropical and temperate moss family Leskeaceae is represented by only one species *Pseudoleskea obtusiuscula* Renault et Cardot. It is the only family represented by only a single species which is endemic.

The moss genera with the largest numbers of endemic species are *Leucoloma* (33 of 55), *Schlotheimia* (16 of 31) and *Macromitrium* (15 of 24) (Figure 8). There are a few genera that are represented by only endemic species: *Entodon* (5 species), *Tortula* (4 species), *Renauldia* (3 species), *Mielichhoferia* (2 species) and *Schizymerium* (2 species). Fourteen moss genera (7.52% of all moss genera) and one liverworts genera are represented in Madagascar by only one endemic species.

Madagascar shows no endemism at the family or genus level for bryophytes. However, of the 4 families endemic to the Sub-Saharan region, i.e. Nanobryaceae, Rutenbergiaceae and Serpotortellaceae (mosses) and Wiesnerellaceae (liverwort), two are found in Madagascar: Rutenbergiaceae and Serpotortellaceae. *Rutenbergia* is represented by 5 species, of which four are endemics of Madagascar (Appendix 1). Serpotortellaceae are known only from Madagascar, La Réunion and Seychelles. Nanobryaceae are not usually recognised, and are usually submerged in *Fissidens*. Wardiaceae are still usually recognised and recently Hypodontaceae are recognised as endemic to the Sub-Saharan region.

Of the 20 genera of mosses endemic to the sub-Saharan Africa region (O'Shea, 1997) (O'Shea 2003), four (*Rutenbergia* (5), *Rhizofabronia* (1), *Schimperella* (1), *Serpetortella* (1)) are represented in Madagascar. Whilst of the 10 endemic liverwort genera in the region, six (*Otolejeunea* (3), *Symbiezidium* (2), *Amazoopsis* (1), *Bryopteris* (1), *Metalejeunea* (1) and *Xylolejeunea* (1)) are present in Madagascar (Wigginton, 2009).

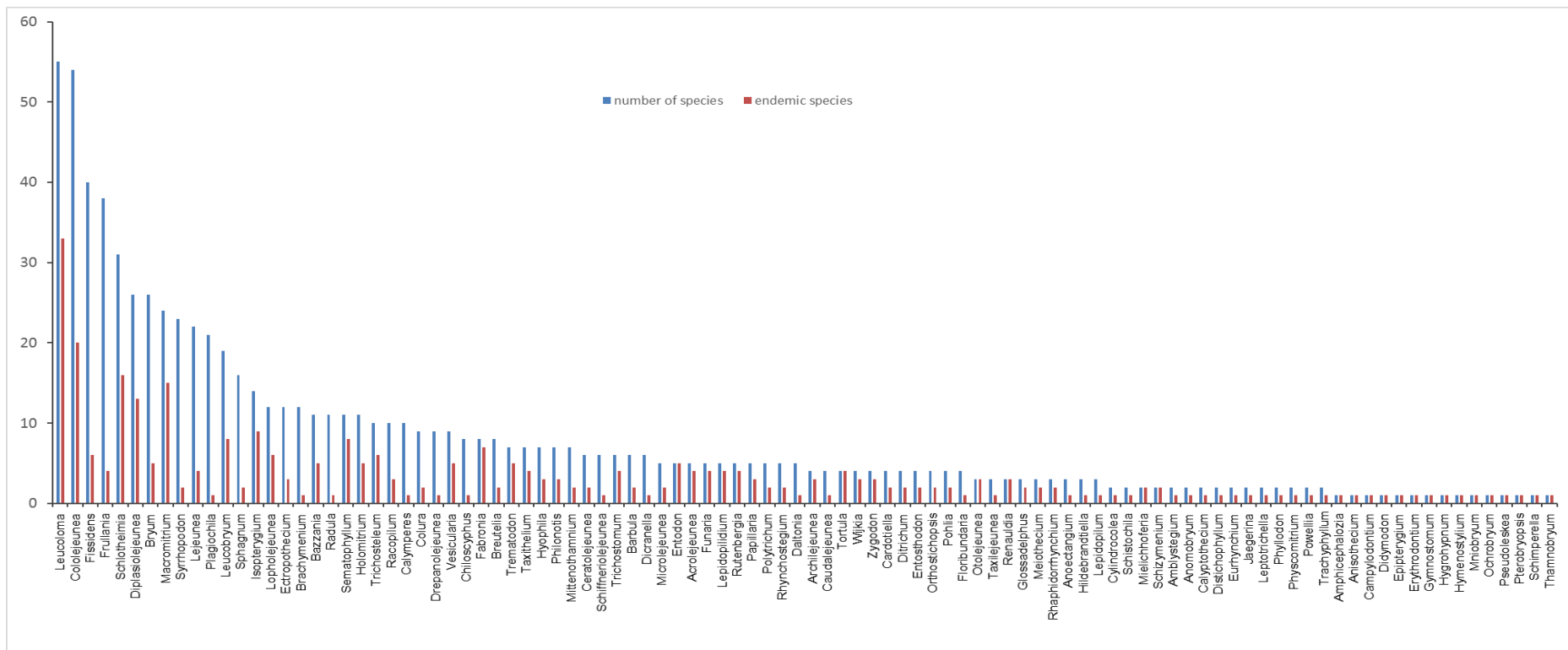


Figure 8: Distribution of endemic liverwort and moss species across genera in Madagascar.

3.3.3. Phylogeographic pattern of the bryophytes of Madagascar

Eight major phylogeographic patterns were recognized for the bryophytes of Madagascar (Table 2): Endemic to the Malagasy Region (sub-endemic) (13%); Endemic to Madagascar (27.61%); African (34%); Paleotropical (6%); Pantropical (12%); Tropical Afro-American Disjuncts (5%); Asian (>1%); Cosmopolitan (1%) (Figure 9, Table A 1).

Table 2: Distribution of Madagascan bryophyte species among nine phylogeographic groups.

Phylogeographic pattern	Number of taxa		
	Total	Liverworts	Mosses
1. Endemic to Madagascar (END)	328	74	254
2. Malagasy Region (sub-endemic) (EMR)	151	51	100
3. African (AFR)	399	149	250
3.a. Tropical African (Trp-Afr)	229	89	140
3.b. Tropical African disjunct			
- Malagasy region + Central African disjunct (<i>MR-CA</i>)	12	4	8
- Malagasy region + Eastern African disjunct (<i>MR-EA</i>)	80	21	59
- Malagasy region + Southern African disjunct (<i>MR-SA</i>)	111	5	6
- Malagasy region + Western African disjunct (<i>MR-WA</i>)	8	3	5
4. Paleotropical (PAL)	70	40	30
5. Pantropical (PAN)	145	63	82
6. Tropical Afro-American Disjunct (Afr-Am)	56	29	27
7. Asian (Afr-As)	5	4	1
8. Cosmopolitan (COS)	9	0	9
9. Pattern unknown (NA)	25	18	7

Phylogeographic pattern are slightly different for liverworts and mosses (Figure 10). Endemics make up a much larger proportion of mosses, whilst African species comprise a much larger fraction of the liverwort flora. The species endemic to the Malagasy region (EMR) make up a higher proportion compared to the pantropical species for liverworts; the opposite pattern is found for mosses. For both mosses and liverworts, paleotropical, tropical Afro-American disjuncts, cosmopolitan and Asian groups are represented by much lower proportions (Figure 10).

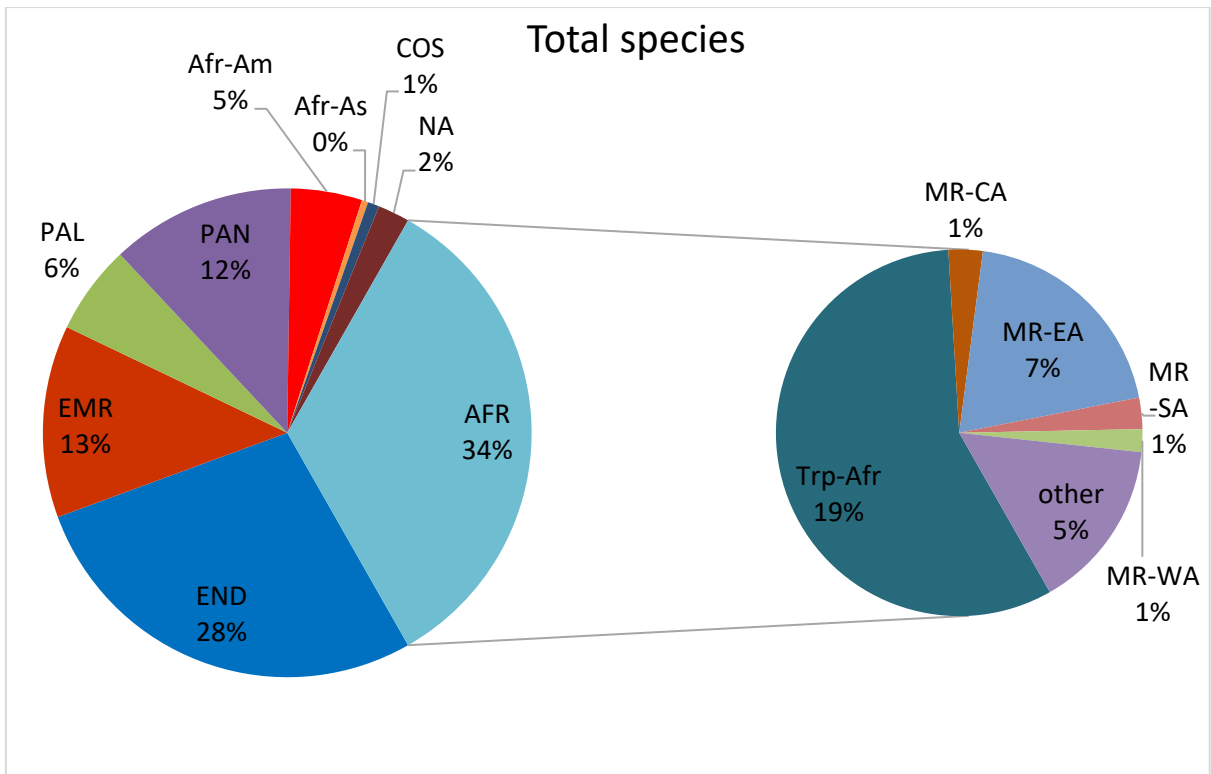


Figure 9: Phylogeographical distribution of the bryophyte flora of Madagascar (END: Endemic to Madagascar, EMR: Malagasy Region (sub-endemic), AFR: African, Trp-Afr: Tropical African, MR-CA: Malagasy region + Central African disjunct, MR-EA: Malagasy region + Eastern African disjunct, MR-SA: Malagasy region + Southern African disjunct, MR-WA: Malagasy region + Western African disjunct, PAL: Paleotropical, PAN: Pantropical, Afr-Am: Tropical Afro-American Disjunct, Afr-As: Asian, COS: Cosmopolitan, NA: Pattern unknown).

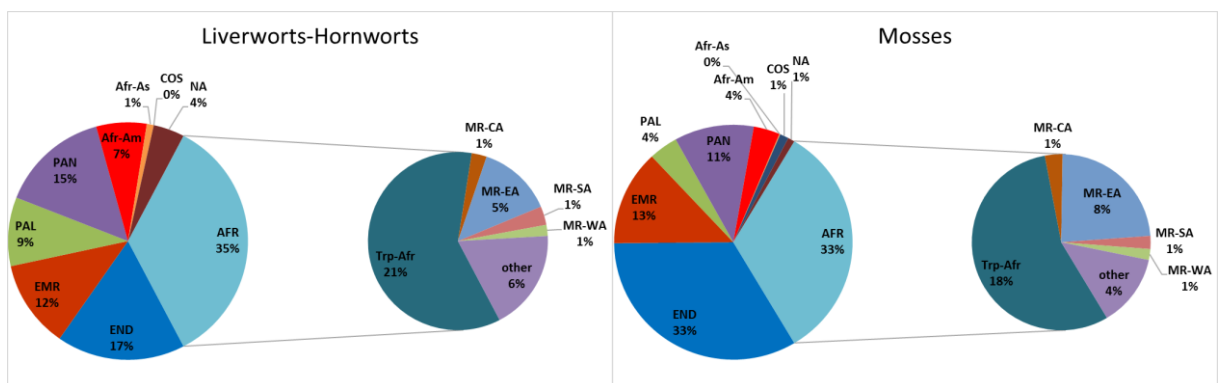


Figure 10: Phylogeographic pattern for mosses and liverworts (END: Endemic to Madagascar, EMR: Malagasy Region (sub-endemic), AFR: African, Trp-Afr: Tropical African, MR-CA: Malagasy region + Central African disjunct, MR-EA: Malagasy region + Eastern African disjunct, MR-SA: Malagasy region + Southern African disjunct, MR-WA: Malagasy region + Western African disjunct, PAL: Paleotropical, PAN: Pantropical, Afr-Am: Tropical Afro-American Disjunct, Afr-As: Asian, COS: Cosmopolitan, NA: Pattern unknown).

(1) Endemic to Madagascar: known distribution does not extend beyond Madagascar. This element represents 27.65% of the Madagascan bryoflora. Examples include the liverwort species *Bazzania decrescens* var. *ambahatrae* Pócs, *Ceratolejeunea saroltae* Pócs, *Cololejeunea diplasiolejeuneoides* Tixier, *Plagiochila fracta* Pócs and the moss species *Breutelia madagassa* var. *madagassa* Thér., *Leucobryum parvulum* Cardot, *Leucoloma marojeziense* La Farge, and *Rutenbergia madagassa* Geh. & Hampe.

(2) Malagasy Endemics (sub-endemic): This category includes species that are restricted to Madagascar and one or more of its neighbouring Islands (La Réunion, Mauritius, Seychelles, Rodrigues or Comoros). Such species represent 12% of the Madagascan bryoflora. The more diverse families that contain sub-endemic species include Lejeuneaceae (25 species), Dicranaceae (19 species) and Orthotricaceae (13 species). Examples include *Bryopteris gaudichaudii* Gottsche, known only from Madagascar and La Réunion, *Leucoloma dichelymoides* (Müll.Hal.) A. Jaeger known for Comoros, Mauritius, Madagascar and Seychelles, *Schlotheimia badiella* Besch., occurring in Mauritius, Madagascar and La Réunion and *Leucobryum comorense* Müll.Hal. which occurs on Madagascar, Comoros and Mauritius. The families represented on the island only by sub-endemic species are Leptodontaceae (*Leptodon fuciformis* (Brid.) Enroth, known for Madagascar, Mauritius and La Réunion) and Serpotortellaceae (*Serpotortella chenagonii* (Renauld & Cardot) W.D. Reese & R.H. Zander, occurring only in Madagascar and La Réunion and *Serpotortella cyrtophylla* (Besch.) W.D. Reese & R.H. Zander, occurring in Madagascar, La Réunion and Seychelles).

(3) African. This category includes species widespread on the African continent and other African islands but otherwise restricted to this area. This is the largest group in the bryoflora of Madagascar comprising 32% of its total bryoflora. The most represented families with more than 20 species are: Lejeuneaceae (55 species), Leucobryaceae (25 species), Dicranaceae (21 species), Fissidentaceae (21 species), and Frullaniaceae (20 species).

The African species may be subdivided into two sub-patterns:

(3a) Tropical African species are more or less continuously distributed all over tropical Africa, including the western African islands and the Indian Ocean islands. Such species comprises 20% of the bryoflora of Madagascar (23% of liverworts and 19% of mosses). Examples include the thalloid liverwort *Riccardia erosa* (Steph.) E.W. Jones and moss species *Tayloria solitaria* (Hedw.) T.J. Kop & W. Weber which are both Tropical

African Montane forest species.

(3b) Malagasy region - tropical African disjunct species are distributed in Madagascar and its neighbouring islands, with a disjunct distribution to some regions of the African continent. The species were subdivided into four subgroups: Malagasy region + Central African disjunct (e.g. *Radula comorensis* Steph.); Malagasy region + Eastern African disjunct (eg. *Leucobryum perrotii* Renauld & Cardot); Malagasy region + Southern African disjuncts (*Pogonatum capense* (Hampe) A. Jaeger); Malagasy region + Western African disjunct (*Frullania gabonensis* Vanden Berghen). They represent 10% of the bryoflora (8% of the liverworts and 11% of the mosses) and 29% of the African species reported for Madagascar. The largest group by far is the Malagasy-East African disjunct, representing 7% (5% of the liverworts and 8% of the mosses) of the bryoflora of Madagascar and 22% (16% of the liverworts and 24% of the mosses) of the African species.

(4) Palaeotropical Element: These species, distributed throughout the African, Asian and Australasian tropics but not the Neotropics, make up 6% of the bryoflora of Madagascar. This element is dominated by the Lejeuneaceae (20 species). Examples of palaeotropical species include the liverwort species *Mastigophora diclados* (Brid. ex F.Weber) Nees and *Pleurozia gigantea* (F.Weber) Lindb. and the moss species *Rhodobryum commersonii* (Schwaegr.) Brid. and *Trachypodopsis serrulata* var. *serrulata* (P. Beauv.) M. Fleisch.

(5) Pantropical species: these species, distributed throughout tropical regions, but sometimes extending into the subtropics, account for 11% of the bryoflora of Madagascar. Examples of pantropical species include *Herpetineuron toccocae* (Sull. & Lesq.) Cardot, *Dumortiera hirsuta* (Sw.) Nees, *Eustichia longirostris* (Brid.) Brid, and *Leucomium strumosum* (Hornsch.) Mitt.

(6) Tropical Afro-American Disjuncts: these species distributions are restricted to the African mainland and its surrounding islands as well as tropical and antipodal America. Such species comprise only 5% of the bryoflora of Madagascar (7% of the liverworts and 4% of the mosses). Examples of this element include *Pilotrichella flexilis* (Hedw.) Aongstr., *Leptodontium pungens* (Mitt.) Kindb., *Fissidens submarginatus* Bruch ex C. Krauss, and *Isotachis aubertii* (Schwaegr.) Mitt.

(7) Asian Elements: These species are mainly distributed in tropical and east Asia from India to Japan and New Guinea. Reaching Africa only in the Malagasy Region, they

represent a very small proportion (<1%) of the flora of Madagascar. Examples of this element include *Gottschea neesii* (Mont.) R.M.Schust., *Lepidolejeunea bidentula* (Steph.) R.M. Schust., *Metzgeria quadrifaria* Steph. *Odontoschisma jishibae* (Steph.) L.Söderstr. and *Bryum neelgheriense* var. *wichurae* (Broth.) Mohamed.

(8) Cosmopolitan Element: These are species that occur more or less globally but may be absent from high mountains and the most extreme alpine and polar regions (3% of the bryoflora of Madagascar). The seven cosmopolitan species recorded for Madagascar are: *Bryum argenteum* var. *argenteum* Hedw., *Bryum caespiticium* var. *caespiticium* Hedw., *Bryum capillare* var. *capillare* Hedw., *Funaria hygrometrica* Hedw., *Hedwigia ciliata* var. *ciliata* (Hedw.) Ehrh. ex P. Beauv., *Leptobryum pyriforme* (Hedw.) Wilson and *Polytrichum commune* var. *commune* Hedw. None of the Madagascan liverwort species has a cosmopolitan distribution.

3.3.4. Comparison between Madagascar and its neighbouring islands

The bryophytes of Madagascar have often been studied together with its surrounding islands. Madagascar's bryophyte species richness as well as endemism appears to be the highest (Table 3). Despite the differences in size and ages of the islands and low similarity, the number of species common to the islands is remarkable, especially between Madagascar and La Réunion (Table 4).

In total 1596 species are recorded for Madagascar and its neighbouring islands. As currently known, 633 species (40%) are endemic to this region. This strongly supports the recognition of this region as a hotspot of biodiversity for bryophytes.

Of the most diversified genera in the Indian Ocean Region, *Leucoloma* has 67 species, 55 of which are recorded from Madagascar with 33 of these endemic to the island. Another example is the liverwort genus *Cololejeunea* with 70 species recorded for the region, 54 of which are reported for Madagascar. The flora of Madagascar includes a certain number of rare genera. For instance, *Caudalejeunea*, one of the rarest genera in the Indian Ocean Islands has 11 species in the Sub-Saharan African region, with only four reported for the Indian Ocean region all of which are confined to Madagascar, with one endangered endemic species *Caudalejeunea grolleana* Gradst.. Another example is the liverwort genus *Otolejeunea* (Lejeuneaceae), which has a total of 9 known species, including three African species, all of which are endemic to Madagascar.

Table 3: Comparison of the bryophyte species richness and endemism between the Indian Ocean Islands.

	Madagascar	La Réunion	Mauritius	Rodrigues	Comoros
Mosses	760	449	247	42	180
Liverworts and Hornworts	428	304	164	30	143
Endemism (%)	27.61	10.8	2.18	2.77	10.21
Total species	1188	753	411	72	323
Size (km ²)	592 800	2 512	1 865	109	2034
Origin (Mya)	130	3	8-10	8-15	0.01 - 7.7
Highest summit (m)	2889	3070	828	398	2361
Minimum distance from Africa (km)	410	2100	2300	2850	300
Minimum distance from Madagascar (km)	-	754	890	1480	550
Type	Continental: rifted from Africa	Oceanic	Oceanic	Oceanic	Oceanic
Bryophyte species richness and endemism(Ah-Peng & Bardat, 2005; O'Shea, 2006; Wigginton, 2009; Marline <i>et al.</i> , 2012); Geographical comparison of the islands (Agnarsson & Kuntner, 2012)					

The bryoflora of Madagascar and La Réunion are the most diverse and the most similar $S_j = 0.307949$ (Table 4), sharing 39.7% of the liverworts and hornworts and 25.1% of the mosses.

Table 4: Matrix of Jaccard's Similarity index, comparing Madagascar, Rodrigues, Mauritius, La Réunion and Comoros.

	MAD	ROD	MAU	REU
ROD	0.020979			
MAU	0.10477	0.11976		
REU	0.307949	0.026634	0.161712	
COM	0.198361	0.032258	0.153477	0.192067
Binary method using the similarity index of Jaccard SD = 0.464544, Mean = 0.314997				

Only seven species of liverworts are common to all five islands: five species of Lejeuneaceae: *Acrolejeunea emergens*, *Cheilolejeunea surrepens*, *Cololejeunea cuneata*, *Lejeunea anisophylla* and *Microlejeunea africana*; *Frullania apicalis* (Frullaniaceae) and *Radula appressa* (Radulaceae).

3.4. Discussion

3.4.1. Place of the bryoflora in the Flora of Madagascar

The bryophyte flora of Madagascar with its 1188 species and infraspecific taxa is relatively rich. Species richness is dominated by mosses (760 mosses vs 425 liverworts), reflecting the global difference in diversity between the two groups. Only 3 hornworts are reported for Madagascar and this is the least documented of all three groups.

3.4.1.1. High endemism

The flora of Madagascar is renowned for its extraordinarily high level of species diversity and distinctiveness (Callmander *et al.*, 2011). It is one of the eight areas in the world with reportedly high species endemism and diversity (Myers *et al.*, 2000). In total, 27.65% of the recorded bryophytes of the island are endemics. Various theories have been proposed to explain the unusually high levels of species diversity and endemism in Madagascar (1) events since the fragmentation of Gondwana during the late Jurassic to upper Cretaceous, other than the 120-160 Mya isolation of Madagascar through continental drift. Long-distance dispersal potentially enables species to maintain transcontinental connectivity between populations (Yoder & Nowak, 2006; Nie *et al.*, 2013). Isolation has had a major influence on the evolutionary history of the flora and fauna. Thus, most bryophyte species present there have evolved in long isolation. (2) Several studies have emphasized that the mountain massifs in the north of Madagascar have a putative function as centres of clade origin and endemism (Raxworthy & Nussbaum, 1997; Andreone *et al.*, 2000; Yoder & Heckman, 2006; Boumas *et al.*, 2007). (3) The island is covered by a diverse array of vegetation habitats (Gautier & Goodman, 2003; Ingram & Dawson, 2005). (4) An alternative hypothesis is the wide barriers to gene flow that could promote lineage diversification (Pastorini *et al.*, 2003; Boumas *et al.*, 2007; Wollenberg *et al.*, 2008; Vences *et al.*, 2009).

In comparison to its neighbouring islands, bryophyte endemism is much higher for Madagascar (Table 3). Globally, the percentage of endemism varies greatly among islands, with the highest percentages often associated with ancient continental islands and the larger and higher oceanic islands in tropical and warm-temperate latitudes (Whittaker &

Fernandez-Palacios, 2007). The size of Madagascar surely contributes to its species diversity and endemism. The Mascarenes and the Comoros, relatively recent volcanic origin, are biologically closely linked to Madagascar, and reveal important endemic biodiversity. Those smaller islands have much smaller floras due to their reduced area and variety of habitats.

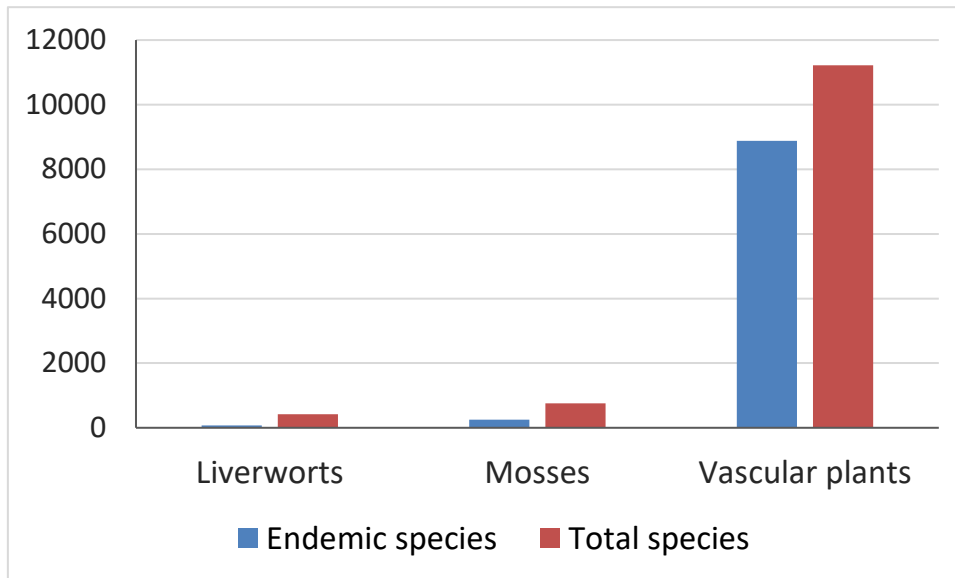


Figure 11: Comparison of species richness and endemism between bryophytes and vascular plants.

Compared to vascular plants, bryophyte endemism is much lower (Figure 11). A study of the endemic and non-endemic species of Madagascar has shown that 84% of the 10,650 vascular plant species recorded for Madagascar, distributed over 1621 genera and 212 families, are endemic (Callmander *et al.*, 2011). Endemic bryophyte species represent only 3.5% of the floristic endemism of Madagascar. This level of endemism, regardless of the existence of numerous undescribed and unrevised species, provides ample support for its status as a global hotspot of biodiversity. Endemism in bryophytes of Madagascar is only found at species level. By contrast, vascular plant endemism can be found up to genus and family level. Isolation seems to have more impact on vascular plants than bryophytes in driving speciation.

Bryophytes show a wide variety of distribution patterns, from very extensive to very narrow ranges (Tan & Pócs, 2000). Nonetheless, not only for Madagascar, but for most cases, bryophytes exhibit endemism in most regions. Compared to bryophytes, vascular plants present a high degree of isolation, both in time and space and short distance dispersal. Many bryophytes could potentially maintain the genetic connectivity between

populations, even if they grow in localities that are several thousand kilometres apart, due to the high dispersal capacity of many species, which could prevent population differentiation even in remote islands. Under such a scenario, allopatric speciation should be relatively rare among bryophytes (Medina *et al.*, 2009). Even if the rate of endemism among bryophytes is lower than that found in vascular plants, there are however many cases around the world where the rates of endemism indicate isolation of the floras. Madagascar is one of the areas that exhibit the world's highest endemism rates for vascular plants (>80%) with a similarly relatively high liverwort and moss endemism of 27.61%. This is also the case for other islands: for example, Hawaii, has 29% endemism for mosses and 48% for liverworts (Staples *et al.*, 2004) and New Caledonia exhibits 50% endemism for mosses and 48% for liverworts (Cox *et al.*, 2001). The levels of endemism for vascular plants for the two islands exceed 70%. With this information, we can infer that biogeographic barriers can have different significance for bryophytes versus vascular plants.

3.4.1.2. Could the high diversity and endemism in the bryophytes of Madagascar be fictive?

Species richness and the percentages of endemism vary extremely from family to family. Interestingly, bryophyte groups that are among the most well documented and recently revised groups from the tropical African region are the most species rich and exhibit high levels of endemism. This is the case for the moss family, Dicranaceae and liverwort family Lejeuneaceae. Of the 83 species of Dicranaceae, 55 species belong to the genus *Leucoloma* (33 endemics/55 species) which has recently been taxonomically revised (La Farge, 2002a, 2002b, 2002c). Lejeuneaceae alone is composed of 203 species. Of the 84 endemic liverwort species, 59 belong to this family. *Cololejeunea* (20 endemic/54 species) and *Diplasiolejeunea* (13 endemics/26 species), both well-revised genera (Tixier, 1985), are the most species rich and present a high number of endemic species.

For some taxonomic groups, for instance the moss families Orthotrichaceae and Sematophyllaceae with high recorded species richness and endemism, actual endemism is difficult to confirm as they have not been revised. However, given the reduction in names in the Orthotrichaceous genera *Macromitrium* and *Schlotheimia* in neighbouring areas (Wilbraham, 2007, 2016), the current numbers could be greatly inflated. Of course, revision could also reveal additional, currently unrecognised endemic taxa.

3.4.2. Phytogeographic affinities of the bryophytes of Madagascar

The affinity of the bryophyte flora of Madagascar and the Indian Ocean islands is fascinating. The most floristically similar to Madagascar seems to be La Réunion and Comoros, whilst Mauritius and Rodrigues, being the oldest islands of the Mascarenes, seem to be more similar to each other than to Madagascar. Despite its younger age (3 Mya), a greater variety of habitats is available on La Réunion due to its high summits and rough topography. The height of the island makes it a bigger “target” for propagules – assuming that migration is from Madagascar to the other islands because of their ages. Migration of species to Comoros in the other hand is facilitated by its proximity to Madagascar and the trade wind direction. In addition, Comoros’s larger islands (Grande Comore and Anjouan), have significant topographic relief supporting lowland, montane rainforests and subalpine vegetation.

The analyses of known bryophyte distribution patterns give a clearer picture on the bryological affinities of Madagascar. The endemic and sub-endemic (endemic to the Malagasy region) groups, make up a very high proportion (43%) of the bryoflora of Madagascar. This is not surprising since, Madagascar has been a major source of colonizing lineages for its neighbouring islands. They share similar environments with relatively small distances between them and Madagascar. Since they are young volcanic islands (0.2-15 Mya) they have not been connected to each other or to Madagascar or other continental areas. This emphasises the role of “waif dispersion” in generating the present-day biodiversity on those islands (Strijk *et al.*, 2012). Thus, the bryophyte colonisation of Madagascar’s younger neighbouring islands is mainly attributed to long distance dispersal (LDD).

The high African affinity (76%) of the bryoflora of Madagascar shows its belonging to the African bryoflora kingdom (Pócs & Geissler, 2002). Some species of the Malagasy region have a disjunct distribution within the African continent. This disjunct pattern is dominated by an affinity with the East African region (7%). It is often seen that bryophyte species have broader geographical ranges extending over more than one continent. The African and intercontinental disjunct distributions observed in bryophytes can be explained by either ancient vicariance via continental drift; or relatively recent LDD (Yoder & Nowak, 2006; Federman *et al.*, 2015). Bryophytes may have been carried along on tectonic plates during continental drift or collision. The proximity to the African continent (400 km) may have affected the dominance of African taxa, through both vicariance and LDD processes. Biotic exchange has likely happened due to dispersal, following the

separation of Africa, Madagascar and India. Through LDD several species are potentially capable of maintaining transcontinental connectivity between populations. The Gondwanan Vicariance is a better explanatory of the existence of pantropical and paleotropical species in Madagascar (Yoder & Nowak, 2006; Nie *et al.*, 2013). **Figure 12** summarises for the bryophytes of Madagascar, the likely intercontinental distribution patterns from Vicariance processes, and dispersal routes via long-distance dispersal agents and processes.

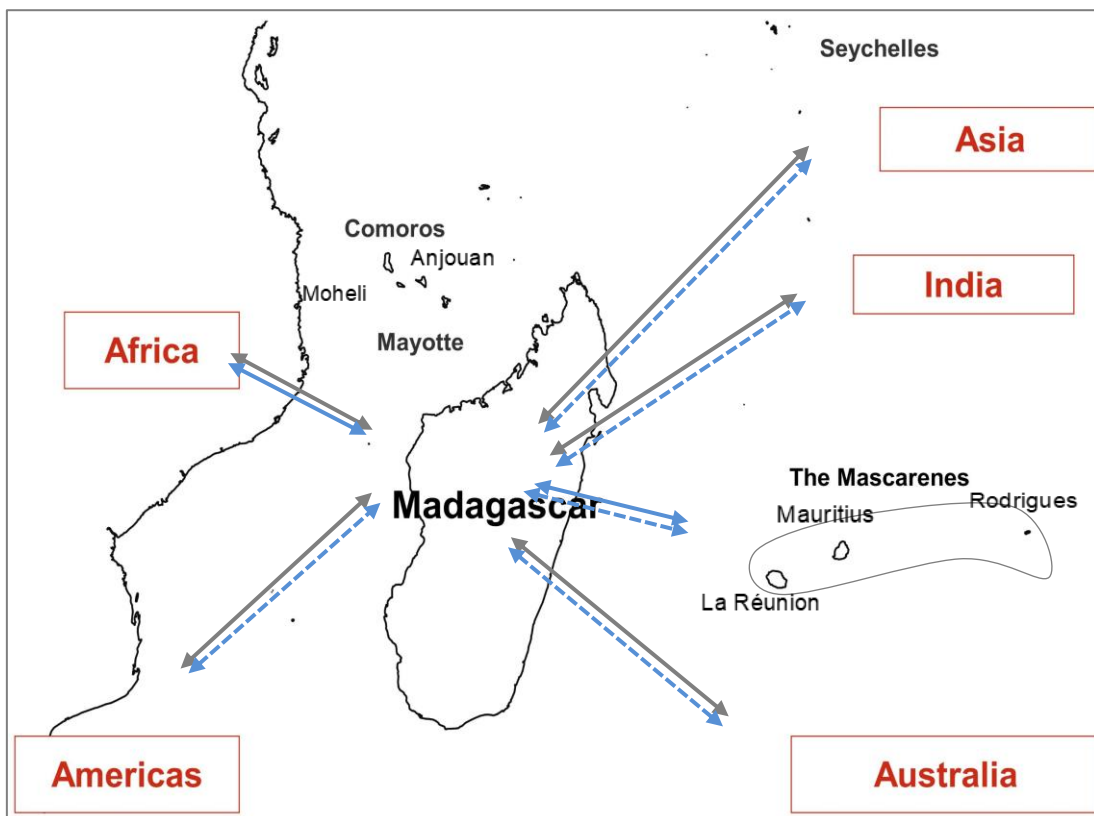


Figure 12: Movement of bryophytes from and into Madagascar. (1) Vicariance processes (grey arrow), for species with Intercontinental disjunct, paleotropical and pantropical distribution patterns. (2) Long-distance dispersal (blue arrow) via (a) bird dispersal from Southeast Asia; (b) marine currents from Southeast Asia; and (c) short-distance dispersal across the Mozambique Channel; and (3) extinction of African relatives. Full arrow (predominant dispersal route), dash arrow (minor dispersal route).

3.4.3. Threats and conservation needs

Many of the forests where bryophytes were collected, in the past no longer exist. Habitat destruction under human pressure is the main threat for the bryoflora of Madagascar. In 2000 alone, 8% of Madagascar's native vegetation disappeared (Harper *et al.*, 2008). In 1996, about 18% of the surface area of Madagascar was still covered by

primary vegetation (Du Puy & Moat, 1996). Since much of the original bryological exploration of Madagascar took place during the late 1800's (Dorr, 1997), it is not known what proportion, if any, of the recorded taxa have been lost due to anthropogenic destruction of habitats for farming and logging (Marline *et al.*, 2012).

Remaining forests of Madagascar are highly endangered by threat of deforestation. The main causes of deforestation in Madagascar are due to cultivation involving slash and burn and illicit exploitation of natural forest. Only 6%, of Madagascar's remaining primary vegetation are officially recognised protected areas (1.17% its total surface) and at least 40% of which is indicated as secondary vegetation (Du Puy & Moat, 1996).

Extending the protected area network is a big challenge for biodiversity conservation in Madagascar. Diversity and endemism of bryophytes has never been considered for conservation matters and planning. However, three species recorded from Madagascar are included in the red list of the IUCN: *Caudalejeunea grolleana* (an endangered endemic), *Symblezidium madagascariensis* (also endangered) and *Bryopteris gaudichaudii* (critically endangered, extinct in La Réunion Island) (<http://www.iucnredlist.org>). No recent studies have dealt with the conservation status of bryophytes. Most of the information we have on the bryophytes of Madagascar is limited to species names, and the absence of detailed geographic data for the vast majority of species make it difficult to design effective conservation strategies. Therefore, this study can be used as a first reference for further study on using bryophytes as basis for conservation planning.

CHAPTER 4

Species richness and range distributions of epiphytic bryophytes along an elevational gradient in Marojejy National Park (Madagascar)

4. Species richness and range distributions of epiphytic bryophytes along an elevational gradient in Marojejy National Park (Madagascar)

4.1. Introduction

Islands represent simplified real-world systems at smaller scales that are globally replicated (Whittaker & Fernandez-Palacios, 2007; Kueffer & María Fernández-Palacios, 2010). Tropical islands are home to extraordinary plant diversity and endemism, especially those with mountain forests with their isolated position and elevational belts (Übersicht *et al.*, 2011; Ah-Peng *et al.*, 2012). The short distances between vegetation types, and the variation in factors such as rainfall intensity, humidity levels, and temperature ranges, cause changes in plant communities along elevational gradients (Rahbek, 2005; Übersicht *et al.*, 2011; Lee *et al.*, 2013; Baumann *et al.*, 2016).

Elevational gradients are especially suited for studying ecological responses of species to climatic and other environmental changes. Furthermore, the distribution of species richness along elevational gradients offers an opportunity to investigate general mechanisms that drive local-scale species diversity patterns (McCain, 2007; Grau *et al.*, 2012).

Bryophytes are important component of tropical mountain rainforests and comprise a significant component of the biomass (Pócs, 1982; Holz & Gradstein, 2005; Gehrig-Downie *et al.*, 2011). They play an important role in the water balance (Ah-Peng *et al.*, 2017) and nutrient cycling of forests (Coxson, 1991; Curtis *et al.*, 2005), and are used as substrate and food source for small organisms such as invertebrates and orchids (Pócs, 1980; Gradstein, 1992). Because of their simple anatomy - lacking roots and complex vascular tissues - and poikilohydry nature, bryophytes are particularly sensitive to environmental changes (Proctor, 2000; Song *et al.*, 2015). In tropical rainforests, bryophytes diversity is mostly dominated by epiphytic communities (Gradstein, 1992). Rich epiphytic bryophyte communities are good indicators of forest quality and integrity in terms of structure and resource availability (Frego, 2007; Song *et al.*, 2015).

Several studies have examined the pattern of bryophyte species diversity and distribution in relation to elevation (Wolf, 1993; Grytnes *et al.*, 2006; Henrik, 2006; Ah-Peng *et al.*, 2007; Grau *et al.*, 2007; Tusiime *et al.*, 2007; Sun *et al.*, 2013; Sanger & Kirkpatrick, 2015; Song *et al.*, 2015). Four distribution patterns are often reported: (1) a

monotonic decrease, (2) a monotonic increase, (3) a hump-shaped distribution with high richness at mid-elevation and (4) multimodality. The hump-shaped pattern is the most commonly reported (Song *et al.*, 2015). The length of an elevational gradient can affect the observed pattern of species richness. For instance, on shorter gradients, a monotonic increase, is the most commonly observed pattern (Spitale, 2016). The hump-shaped or multimodal patterns are more common on longer gradients (Grau *et al.*, 2007; Ah-Peng *et al.*, 2012; Sun *et al.*, 2013).

The main drivers of elevational diversity patterns remain controversial. On one hand, climatic variables have been shown to play important roles in certain system (Bhattarai *et al.*, 2004; Sanders *et al.*, 2007; Whittaker *et al.*, 2007). Climate directly controls the range distribution of individual species if species physiological tolerances are exceeded in parts of the gradient (Rowe, 2009; Tang *et al.*, 2014). It is assumed that optimum environmental conditions for epiphyte growth and survival include favourable moisture conditions due to cloud cover, precipitation and lower temperature (Sanger & Kirkpatrick, 2015). On the other hand, habitat heterogeneity influences the production and maintenance of diversity by providing more resources and therefore supports a larger number of species (Ricklefs, 1977; Tilman & Pacala, 1993; Kadmon & Allouche, 2007). Recently, various studies have found that bryophytes distribution patterns along elevational gradients are correlated with climatic factors such as temperature, humidity and rainfall (Porley & Hodgetts, 2005), suitable substrates (Gabriel & Bates, 2005; Song *et al.*, 2015) and vegetation structure (Evans *et al.*, 2012).

An alternative null model of distribution pattern is the mid-domain effect (MDE) (Colwell & Lees, 2000). The MDE predicts a mid-gradient peak in richness resulting from an increased overlap of species ranges towards the centre of a shared geographic domain. This is due to geometric boundary constraints in relation to the species distribution ranges and midpoints (Colwell & Hurtt, 1994; Colwell *et al.*, 2004). Colwell *et al.* (2004) predicts that the mid-gradient peak in richness is affected by large-ranged species rather than small-ranged species. Recent studies suggest that the MDE is a powerful explanatory predictor of elevational patterns in bryophyte species richness in some contexts (Ah-Peng *et al.*, 2012; Gabriel, Bardat, *et al.*, 2014; Henriques *et al.*, 2016).

Continental islands like Madagascar are good candidates for elevational gradients studies in species richness. Not only are they larger in area, geologically older and reach higher elevations but also biologically more similar to mainland areas in terms of species taxonomy (Irl, 2016). Whilst the diversity and distribution of Madagascan vascular plants

and ferns along elevational and other gradients have received considerable attention, bryophytes have rarely been considered (Messmer *et al.*, 2000; Rakotonrainibe, 2000; Pócs & Geissler, 2002; Goodman & Benstead, 2004). Knowledge of the ecological mechanisms explaining the richness and distribution of bryophytes along elevational gradients thus remains incomplete. This study focuses on the epiphytic bryophytes collected along an elevational gradient in Marojejy National Park, northern Madagascar. It comprises the first elevational survey of bryophytes in Madagascar using a standardised ecological sampling method. The main objectives are: (1) to describe bryophyte species composition and endemism in Marojejy National Park; (2) to describe the species richness and distribution patterns of epiphytic bryophytes along an elevational gradient and, (3) to evaluate environmental variables as explanatory factors for the observed elevational patterns and evaluate the importance of the mid-domain effect in explaining bryophyte species richness in this system.

4.2. Materials and Methods

4.2.1. Study area

This study was carried out in Marojejy National Park, located in the Sava region of north-eastern Madagascar, between Sambava and Andapa (Figure 13). It covers 55,500 ha of land, and protects the entire massif of the same name. Due to the steep slopes, the massif has rugged topography rising quickly from the Indian Ocean, to the escarpment of the massif, with the highest peak at 2132 m above sea level (asl). The northern side of the massif has a gentle slope toward the peak, with steep slopes on the south sides. Marojejy is underlain by Precambrian basement rocks (Goodman, 2000b).

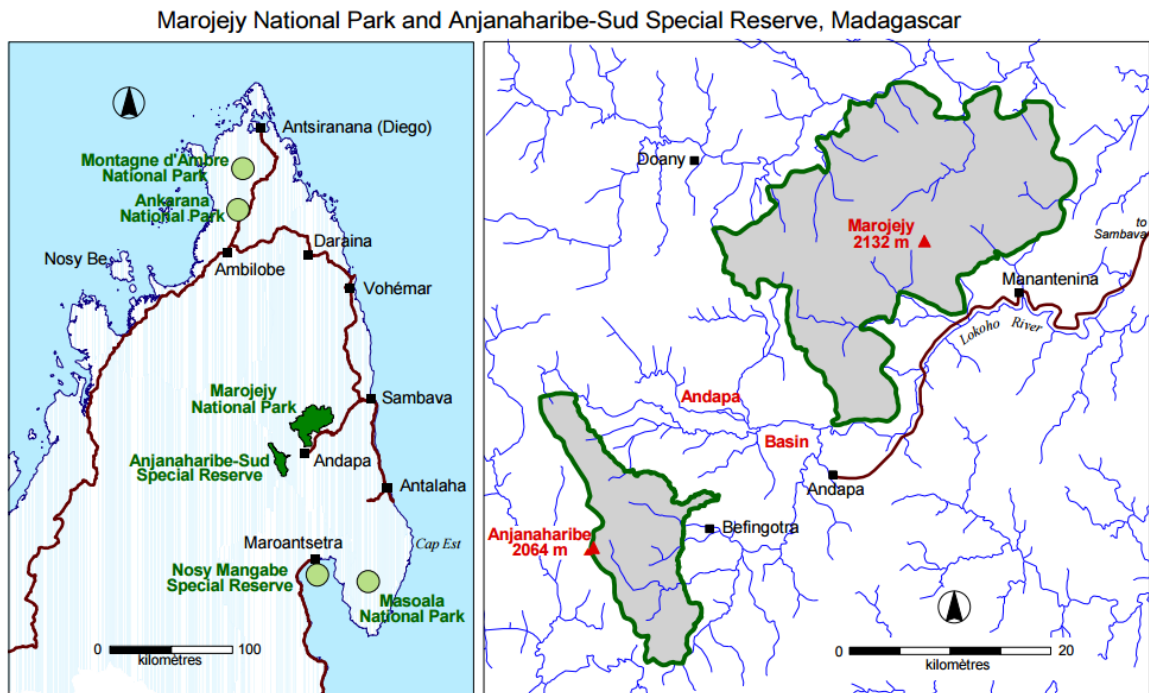


Figure 13: Location of Marojejy National Park, North-eastern Madagascar (http://www.marojejy.com/Cartes_e.htm).

The climate is primarily defined by the regional trade wind patterns, and the rains transported by these winds. The periodic cyclones and heavy rain during the warmer season (November-April) are brought by the Monsoons from the northwest. The trade winds from the east carry light, variable rains with rare storms during the cooler season (May-October), (Goodman, 2000b). On the eastern windward slopes, the rainfall is notably higher than in the western leeward slopes. The mean annual precipitation recorded from the nearest weather stations is 2296 mm at Sambava (10 m) and 1883 mm at Andapa (530 m). The mean annual temperature varies from 13.5 to 31.6 °C (Goodman, 2000b). Higher rainfall and lower minimum temperatures are observed near the peaks.

Forests cover 90% of the Marojejy National Park, are unevenly distributed and show much variation.

-Below 800 m, Evergreen Rainforest occurs – they are sheltered from strong winds under conditions of consistent warm temperatures and abundant rainfall. With canopy height of 25 to 35 m, the dense evergreen forests are home to many palms, ferns, and epiphytes. Secondary growth in disturbed areas consists primarily of bamboo, wild ginger and Ravinala.

-Medium-altitude Rainforest at 800-1400 m, occurs under conditions of cooler temperatures and impoverished soils, resulting in a lower canopy at 18 to 25 m. Shrubs,

herbaceous forest species, and epiphytes exploit the higher light levels, and the high relative humidity encourages the growth of mosses and ferns.

-High-altitude Montane Cloud Forest at 1400-1800 m, experiences lower temperatures and easterly winds causing heavy cloud cover. Forest canopy height is much reduced to 10 m, with trees short, gnarled and stunted, and their branches draped with mosses and lichens.

-High-altitude Montane Scrub occurs above 1800 m – the windy and cool conditions, lower rainfall, and thin rocky soils are limiting the vegetation to dense thickets of shrubs, forming an open, tundra-like cover home to miniature palms and bamboos, as well as terrestrial orchids. This is the only remaining intact montane scrub in Madagascar (Goodman, 2000b; Garreau & Manantsara, 2003).

The Marojejy National Park with its rich forest habitats houses an exceptionally rich and unique biota (Garreau & Manantsara, 2003). Most species occurring there are endemic to Madagascar, indeed, many are endemic at a regional level. However, many groups of organisms, including bryophytes, are still very poorly documented.

The Marojejy area is a last refuge for many species of plants and animals that once thrived throughout north-eastern Madagascar. The surrounding lowland is one of the most densely populated areas in Madagascar with high population growth rates. This causes high and increasing human pressure on the park with most of the area being deforested. Populations of some species, such as the Silky Sifaka, are on the brink of extinction (Patel *et al.*, 2005). Resource use at greater or lesser extent over the last few decades, includes hunting, and small-scale collection of forest products such as firewood and construction material. During the 1970s, people moved deep into the park, burning significant tracts of forest for growing crops (Goodman, 2000b; Atkinson & Mathieu, 2008).

In 1952, Marojejy was added to one of the strict nature reserves of Madagascar. Under this protection, only research scientists were permitted to visit the site. Later in 1998, it was converted into a national park and thus became open to visitors (Atkinson & Mathieu, 2008). Due to the threats to its biodiversity (illegal logging and trafficking of valuable hardwoods) and its amazing biodiversity, the massif was listed as a World Heritage Site as part of the Rainforests of the Atsinanana in 2007 (IUCN, 2007). Since 2009, the Rainforest of the Atsinanana was added to the list of World Heritage sites in Danger (IUCN, 2009).

4.2.2. Bryophyte sampling and identification

Bryophytes samples were collected in November 2009, following the *Bryolat* protocol (Ah-Peng *et al.*, 2007, 2012; Gabriel, Coelho, *et al.*, 2014), a nested design with four hierarchical levels (i.e. four spatial scales): elevational belts (stations), plots, quadrats and microplots (substrates) (Figure 14).

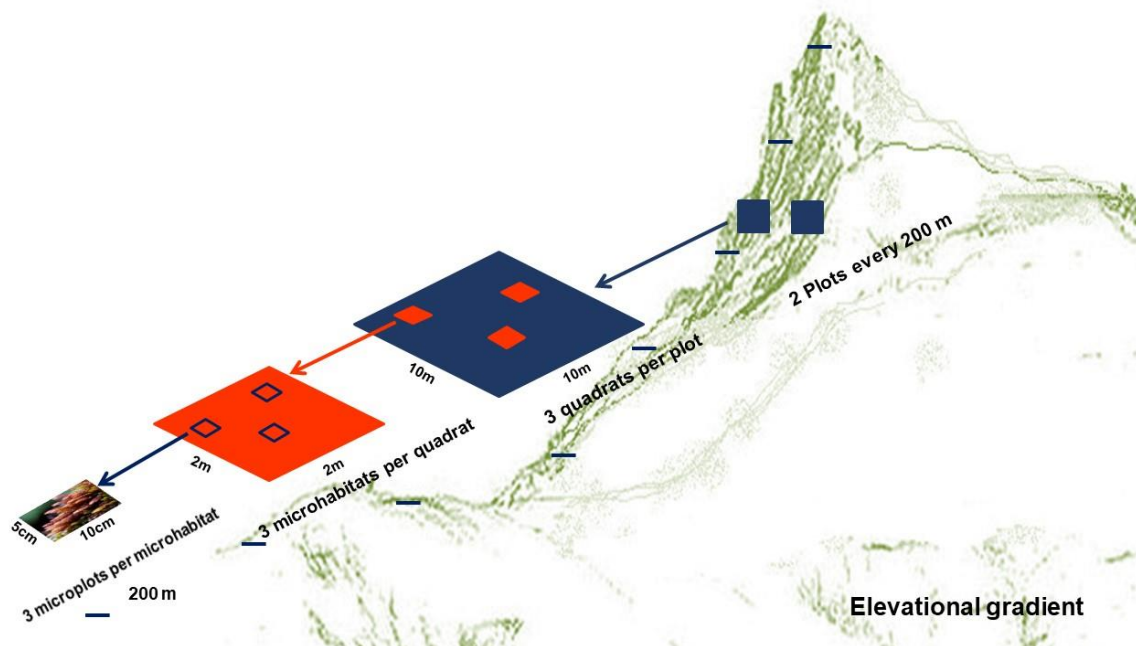


Figure 14: Bryophytes sampling design from Ah-Peng *et al.* (2007), illustrated in Gabriel, Coelho, *et al.* (2014) (transect from low altitude to the summit).

Sampling plots were established at each elevational step of 200 m. The transect started near the east entrance of Marojejy NP and ran to the summit (250 to 2135 m), giving a total of ten studied elevations. Two plots of 10 x 10 m (P1, P2) were set up at each elevational level; the physical characteristics of each plot are given in Table 5. In each plot, three quadrats of 2 x 2 m (Q1, Q2, Q3) were randomly chosen. Within each quadrat, three trees were randomly chosen and epiphytic bryophyte samples of 5 x 10 cm (microplots) were collected at three heights (microhabitats) TA: 0-50 cm, TB: 50-100 cm and TC: 100-200 cm (Figure 14). Samples were air-dried in the field. Each sample was marked with the altitude, plot number, quadrat number and microplot number (example: 250P1Q1TA1). The total diversity in each microplot sample of 50 cm², as well as the abundance (% cover) of each species present, was determined in the lab.

Since no general key exists for the bryophytes of Madagascar, available literature and herbarium collections were used as references. The most important for mosses were

De Sloover (2003), and La Farge's revision of *Leucoloma* (La Farge, 2002a, 2002b, 2002c). For liverworts, the most important literature included the flora of western Africa (Jones, 2004), and Tixier's (1985) revision of *Cololejeunea* and *Diplasiolejeunea*, Vanden Berghen's revision of some African genera (Vanden Berghen, 1950a, 1950b, 1951, 1981, 1984) and the liverwort and hornwort flora of the Mascarenes (Ah-Peng & Bardat, unpublished). Species nomenclature follows Marline *et al.* (2012) with recent taxonomical modifications for liverworts from the world checklist of hornworts and liverworts (Söderström *et al.*, 2016).

4.2.3. Climatic data and vegetation sampling

A temperature and relative humidity data logger (MadgeTech Data Logger RHTemp1000) was set up at each of five elevational levels in December 2013 (450, 850, 1250, 1650 and 2050 m). These sensors continuously recorded temperature and relative humidity every hour between December 2013 and December 2014. A calibration curve against elevation was used to estimate temperature and relative humidity for sites lacking loggers.

For each site, Vapour Pressure Deficit (VPD), was calculated as the saturated vapour pressure (SVP) in air minus the actual vapour pressure (VP) (Monteith & Unsworth, 2013). If $SVP \text{ (Pascals)} = 610.7 \times 10^{7.5T(237.3+T)}$ and $VP = (RH \times SVP)/100$ where T is temperature (°C) and RH is the relative humidity (%), the following formula is applied to calculate VPD $(\frac{100-RH}{100}) \times SVP$.

For each sampling site, the vegetation type and canopy height (minimum and maximum) were recorded. Vegetation classification follows Humbert's classification of the vegetation of Madagascar (Humbert, 1965). Environmental characteristics of each plots are presented in [Table 5](#).

4.2.4. Data analyses

4.2.4.1. Species accumulation curves

To assess how effectively species diversity was sampled at each elevational site, species accumulation curves (sample-based rarefaction) were used (Gotelli & Colwell, 2001). This method plots the cumulative number of species discovered at each elevational interval as a function of the number of samples examined at that elevation. The order in which samples were added to the species accumulation curve was randomized 100 times to remove order-dependent idiosyncrasies that may arise due to sampling error and

heterogeneity among the units sampled. The method “rarefaction” was applied, since it estimates species richness and its standard deviation by sampling individuals rather than sites (Oksanen *et al.*, 2015). Estimates of species richness are assumed to be accurate if the species accumulation curve reaches a plateau. Species curves were generated using the R function *specaccum* from the package *vegan* (Oksanen *et al.*, 2015).

4.2.4.2. Species richness pattern

To evaluate the distribution pattern of species richness along the elevational gradient, polynomial regressions were performed. Quadratic and linear models were compared by the Akaike Information Criterion (AIC), and the model with the lowest AIC value was selected. In addition to the total bryophyte diversity, mosses and liverworts were analysed separately, as were the three epiphytic microhabitats (TA, TB, TC).

Ecological sampling is rarely, if ever, complete for natural communities (Colwell & Coddington, 1994; Chao *et al.*, 2005; Walther & Moore, 2005), particularly in species-rich systems such as tropical rainforests. Thus, three non-parametric species richness estimators, the bias-corrected Chao (S_{Chao}), the first order Jackknife (S_{Jack1}) and the abundance-based coverage estimator (S_{ace}), were used to estimate species richness from sites (Colwell & Coddington, 1994). All three methods use the frequencies of species in a single site and information on the frequency of rare species in a sample. Both S_{Chao} and S_{Jack1} estimate richness by adding a correction factor to the observed number of species. These methods are known to be less sensitive to detection probabilities and uneven distribution of species (Hortal *et al.*, 2006) and are suitable for community data containing many rare species (Colwell & Coddington, 1994).

S_{Chao} is calculated as $S_{Chao} = S_{Obs} + \frac{a_1(a_1-1)N-1}{2(a_2+1)N}$ where S_{Obs} is observed number of species in the collection, a_1 and a_2 are the number of singletons and doubletons in the collection and N is the number of sites in the collection.

S_{Jack1} is calculated as $S_{Jack1} = S_{Obs} + a_1 \frac{(N-1)}{N}$ where S_{Obs} is observed number of species in the collection, a_1 is number of singletons and doubletons in the collection and N is the number of sites in the collection.

S_{ace} is calculated as $S_{ace} = S_{abund} + \frac{S_{rare}}{C_{ace}} + \frac{a_i}{C_{ace}} \gamma_{ace}^2$

Where $C_{ace} = 1 - \frac{a_i}{N_{rare}}$ and $\gamma_{ace}^2 = \max \left[\frac{S_{rare} \sum_{i=1}^{10} i(i-1)a_i}{C_{ace} N_{rare} (N_{rare}-1)} \right] - 1.0$, a_i : number of species with abundance I, S_{abund} : number of abundant species, S_{rare} : number of rare species and N_{rare} : number of individual in rare species

Polynomial regressions and species richness estimators were computed using the *lowess* function of the package *stats* and the function *specpool* of the *vegan* packages in R (Oksanen *et al.*, 2015; R Core Team, 2015).

4.2.4.3. Species range distribution and geometric constraints

Species elevational range distribution was estimated by subtracting the minimum from the maximum elevation at which the species was recorded (Ah-Peng *et al.*, 2012), assuming that a species is present or potentially present at all elevations between the extremes. The midpoint of a species was measured as the mean of the maximum and minimum elevations at which it was recorded. Species detected at only one elevational sites were assigned an range distribution of 100 m (Ah-Peng *et al.*, 2012).

To test the possible influence of geometric constraints on species richness patterns along the elevational gradient, MDE null model predictions were used. The MDE null distribution was calculated using a Monte Carlo based simulation programme, applying 1000 permutations without replacement (Mid-Domain Null Programme, McCain, 2004). In order to test Colwell *et al.* (2004)'s prediction on the effect of large-ranged and small-ranged species on the mid-domain effect, analyses were run on the full data set as well as individually on small-ranged and large-ranged species. Species covering half the studied domain (1000 m or more) are considered large-ranged species, and small-ranged species are those having an altitudinal distribution covering less than 1000 m. Empirical species richness were regressed against the mean predicted richness values from the null model. The 95% randomization curves outputs were obtained from 50,000 of Monte Carlo simulations with the number of bins fixed at 10 (corresponding to the number of elevational sites).

4.2.4.4. Explanatory variables

A multiple Generalised Linear Models (GLM), with Poisson error distribution and logarithmic links, was used to test how well these explanatory variables predict the species richness patterns. Environmental variables including vegetation type (vege), average canopy height (cmea), mean temperature (temp.m), mean relative humidity (rh.m), vapour pressure deficit (vpd) and Mid domain effect (MDE) acted as causal variables and

species richness at each elevation was the response variables. The best model was selected from the 127 possible outcomes representing all possible combinations of the candidate explanatory variables (vege, cmea, temp.m, rh.m, vpd and MDE), guided by the lowest Akaike information criterion (AIC) (Model 1). Since MDE was correlated with species richness, another multiple Generalised Linear Model (GLM) excluding MDE was computed, where the best model was selected from all possible outcomes representing all possible combinations of the candidate explanatory variables (vege, cmea, temp.m, rh.m and vpd), guided by the lowest AIC (Model 2). Statistical significance of each variable in the models was tested by the z statistic.

Analyses of variance (ANOVA) were used to test for the effects of environmental variables in shaping the pattern of species richness.

Linear models can only be used when the relationship between diversity and potential explanatory variables is linear. They are not suitable for plausible scenarios where a unimodal model is biologically more reasonable (Yu *et al.*, 2013). Thus, I also included a second-degree polynomial regression, to detect whether the relationships between environmental variables (except for vegetation type) and species richness is curvilinear.

Linear models, regression analyses and ANOVA were computed in R software (R Core Team, 2015)

Table 5: Description of environmental conditions at each plot along the elevational gradient in the Marojej National Park.

Plot	Altitude (m)	Geographic coordinates	Vegetation type	Canopy height (m)			VPD (Pascal)	Temperature (°C)			Relative humidity (%)		
				max	min	mea		max	min	mea	max	min	mean
250P1	250	S14°27'11.7" E49°47'32.0"	Low altitude evergreen Rainforest	31	18	24.5	83.50						
250P2	250	S14°27'11.5" E49°47'32.0"	Low altitude evergreen Rainforest	31	18	24.5	83.50						
450P1	491	S14°26'12.3" E49°46'31.3"	Low altitude evergreen Rainforest	25	18	21.5	82.95	31.6	14.7	22.2	100	49.5	96.9
450P2	463	S14°26'12" E49°46'30.4"	Low altitude evergreen Rainforest	25	18	21.5	82.95	31.6	14.7	22.2	100	49.5	96.9
650P1	658	S14°26'17.2" E49°46'07.5"	Low altitude evergreen Rainforest	25	15	20	78.54						
650P2	658	S14°26'16.9" E49°46'07.6"	Low altitude evergreen Rainforest	25	15	20	78.54						
850P1	871	S14°26'16.96" E49°45'25.1"	Mid altitude Rainforest	25	15	20	74.35	30.9	14.4	19.9	100	41.05	96.8
850P2	891	S14°26'16.78" E49°45'24.53"	Mid altitude Rainforest	25	15	20	74.35	30.9	14.4	19.9	100	41.05	96.8
1050P1	1080	S14°26'22.69" E49°45'17.53"	Mid altitude Rainforest	20	14	17	71.49						
1050P2	1065	S14°26'13.1" E49°46'14.6"	Mid altitude Rainforest	20	14	17	71.49						
1250P1	1250	S14°26'11.5" E49°44'44.0"	Mid altitude Rainforest	15	10	12.5	25.99	27.5	10.9	17.5	100	59.0	98.7
1250P2	1258	S14°26'15.5" E49°44'46.7"	Mid altitude Rainforest	15	10	12.5	25.99	27.5	10.9	17.5	100	59.0	98.7
1450P1	1447	S14°26'20.86" E49°44'29.5"	High altitude montane cloud forest	15	5	10	26.41						
1450P2	1487	S14°26'20.8" E49°44'29.8"	High altitude montane cloud forest	15	5	10	26.41						
1650P1	1667	S14°26'39.3" E49°44'17.1"	High altitude montane cloud forest	15	5	10	143.36	30.0	10.6	17.0	100	27.5	92.6
1650P2	1645	S14°26'31" E49°44'18"	High altitude montane cloud forest	15	5	10	143.36	30.0	10.6	17.0	100	27.5	92.6
1850P1	1862	S14°26'41" E49°44'11"	High altitude Montane Scrub	5	2.5	3.75	149.42						
1850P2	1850	S14°26'41" E49°44'12"	High altitude Montane Scrub	5	2.5	3.75	149.42						
2050P1	2050	S14°26'52" E49°44'00"	High altitude Montane Scrub	2	0.5	1.25	148.19	30.0	8.0	16.1	100	24.5	91.9
2050P2	2050	S14°26'52" E49°44'00"	High altitude Montane Scrub	2	0.5	1.25	148.19	30.0	8.0	16.1	100	24.5	91.9

4.3. Results

4.3.1. Species composition

A total of 457 (50 cm²) samples were collected along the elevational transect, yielding 2454 species identifications (Figure 15). Over most of the gradient, approximately equal numbers of samples were collected from the three microhabitats - i.e. the target number was achieved in most instances. The only exception is for the site at 2050 m, where there were no high trees, and thus no samples above 50 cm (TB and TC) were recorded (Figure 16).

Epiphytic bryophyte richness ranged from 1 to 30 species per microplot of 50 cm². In total 254 species, comprising 157 liverworts and 97 mosses, (representing 39 families and 85 genera) were identified. Twenty-three (8.92%) of those species are endemic to Madagascar. Endemic species mostly belong to the moss family Dicranaceae (9) and the liverwort family Lejeuneaceae (7). The most speciose moss families are Dicranaceae (29 species), Orthotrichaceae (16 species), Sematophyllaceae (13 species) and Calymperaceae (11 species). Liverworts are dominated by members of the Lejeuneaceae (73 species), Lepidoziaceae (19 species), Frullaniaceae (15 species) and Plagiochilaceae (11 species). Generally, the number of liverworts is higher than that of mosses at each elevation (Figure 18). Thirty nine species (nine mosses and thirty liverworts) are newly reported for the bryoflora of Madagascar (Appendix 2, Table A 2).

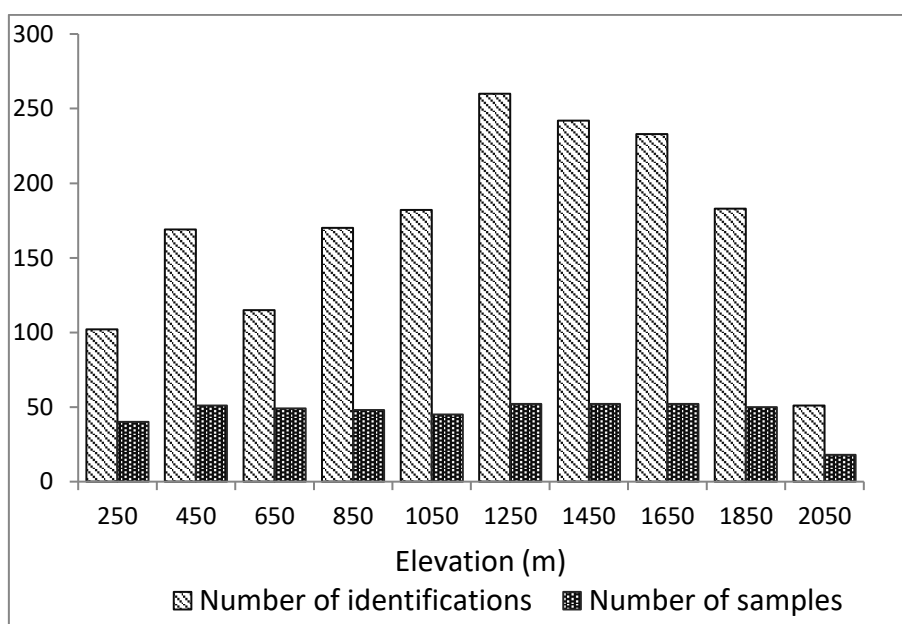


Figure 15: Numbers of microplots (50 cm²) and number of identifications made at each elevation.

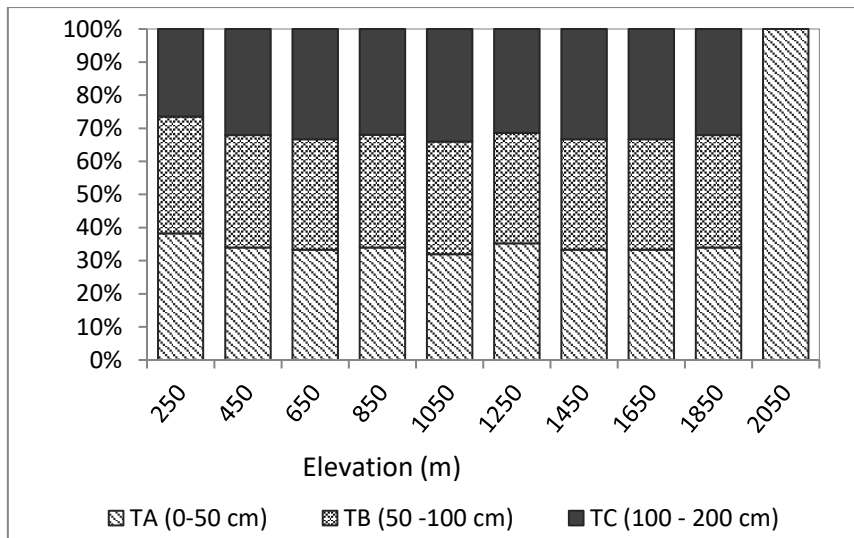


Figure 16: Proportion of sampled microhabitat TA (0-50 cm), TB (50-100 cm) and TC (100-200 cm).

Despite the extensive sampling effort none of the species accumulation curves reached a plateau, but most showed a clear slowdown in the rate of species accumulation after ca 10-12 samples (Figure 17).

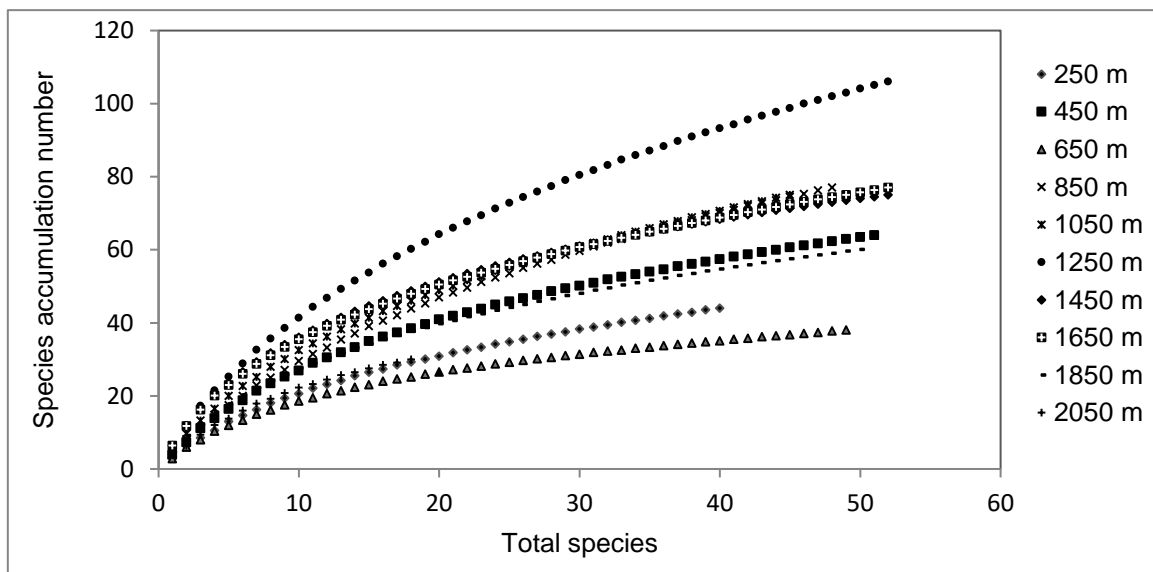


Figure 17: Cumulative number of species (y-axis) plotted as a function of the cumulative number of samples (x-axis), pooled in random order.

4.3.2. Bryophytes species richness pattern along the elevational gradient

4.3.2.1. Species richness pattern

All species richness plots showed a hump-shaped patterns along the elevational gradient. Both overall species and liverwort richness peak at 1250 m and species richness is lowest at 650 m and 2050 m. Moss species richness is highest at 450 m and 1250 m and lowest at 250 m and 2050 m (Figure 18).

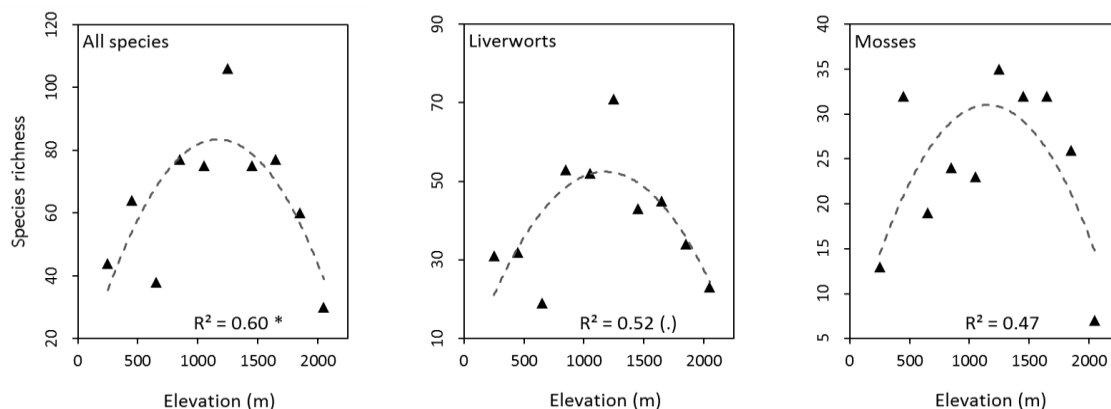


Figure 18: Species richness per elevational interval of 200 m for all species, mosses, and liverworts with second order polynomial trend lines (grey dotted lines). (.) p-value < 0.1, * p-value < 0.05

With respect to the epiphytic microhabitats, all three-studied microhabitats show a different pattern. For TA (0-50 cm), bryophyte species richness showed a slow increase from 250 to 1050 m, reached a mid-elevational peak at 1250 m, and then decreased at higher elevation from 1650 m. For TB (50-100 cm), species richness shows a slower increase and peaks at 1650 m. Whereas, for TC (100-200 cm), bryophytes species richness showed a steeper increase with altitude between 250 and 1050 m, reached a mid-elevational peak at 1250 m, and then decreased rapidly towards high elevation (Figure 19). Both species richness for TB ($R^2 = 0.5765$, $p = 0.0176$) and TC ($R^2 = 0.3235$, $p = 0.0176$) show a significant positive linear relationship with elevation (Table A 3).

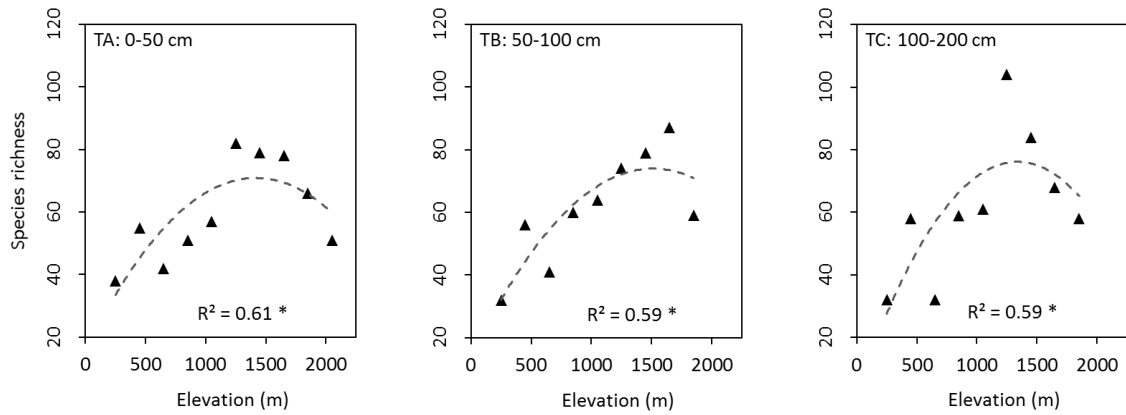


Figure 19: Species richness per elevational interval of 200 m for the different microhabitats: TA (0-50 cm), TB (50-100 cm) and TC (100-200 cm). Second order polynomial trend lines (grey dotted lines). (.) p-value < 0.1, * p-value < 0.05

4.3.2.2. Species richness estimation

All estimates of bryophytes species richness display a similar pattern to the observed richness along the elevational gradient, with a hump-shaped pattern and richness peaking at mid-elevation, 1250 m (Figure 20).

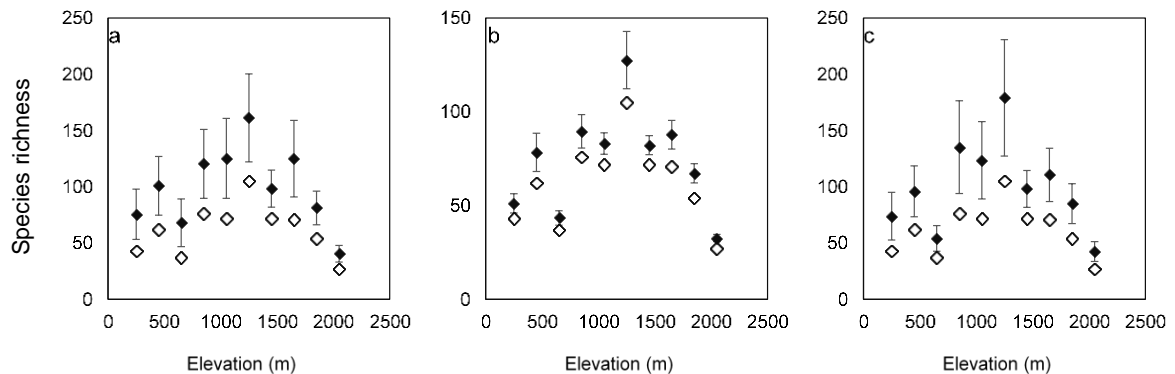


Figure 20: Elevational pattern of observed species richness (open diamond) and richness estimates (filled diamond) with standard deviation of epiphytic bryophytes along the elevational gradients (a) S_{Chao} = bias-corrected Chao, (b) S_{Jack1} = first order Jackknife, (c) S_{ace} = abundance-based coverage estimator.

All diversity estimators yielded higher values than the observed species richness at each elevational band. However, the results from the Jackknife are closest to the observed richness with the lowest standard deviation, whilst ACE shows the highest estimated values as well as the highest standard deviations. The regressions of the estimated richness against elevation (S_{Chao} : $R^2 = 0.6151$, $p < 0.05$; S_{Jack1} : $R^2 = 0.5472$, $p < 0.1$, S_{ace} : $R^2 = 0.5419$, $p < 0.1$) indicate that the sampling was insufficient to precisely characterize the elevational pattern of species richness along the gradient.

4.3.3. Species range distribution and variation along the gradient

The elevational ranges of each individual liverwort and moss species along the transect are shown respectively in [Figure 21](#) and [Figure 22](#). Eighty seven percent of the total recorded species fall into the small-ranged category, including 91% of the mosses and 84% of the liverworts. Only 24 liverworts and 9 mosses exhibit ranges equal to or larger than 1000 m. Only one liverwort species *Lopholejeunea multilacera* Steph., is found from 250 m to 2050 m (range equal to 1800 m). Singletons, restricted to single elevations, comprise 36% (63 liverworts and 40 mosses) of the recorded species. Nine percent of the singleton species (11 liverworts and 12 mosses) are found at 1250 m. Species richness is significantly correlated with the number of singleton species ($R^2 = 0.6982$, $p < 0.005$).

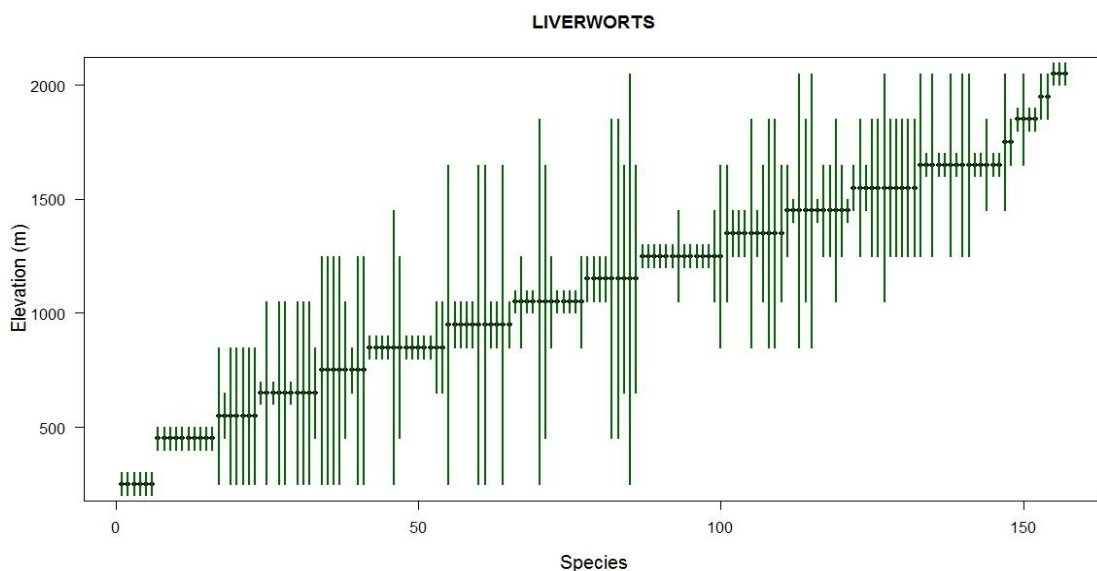


Figure 21: Elevational range profiles of the 157 liverwort species collected on the Marojejy elevational gradient. Black dots show the mean altitudinal occurrence of each species whilst bars indicate the total elevational range.

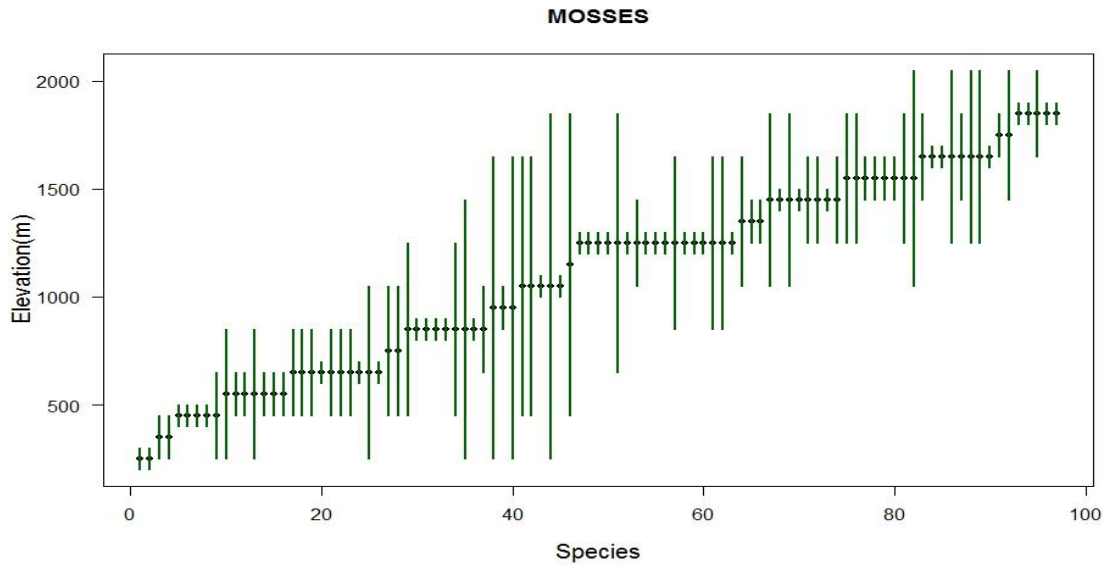


Figure 22: Elevational range profiles of the 97 moss species collected on the Marojejy elevational gradient. Black dots show the mean altitudinal occurrence of each species whilst bars indicate the total elevational range.

In general, there is a decreasing elevational range with increasing elevation. At both end of the elevational gradient, species mean elevational range decline (Figure 23).

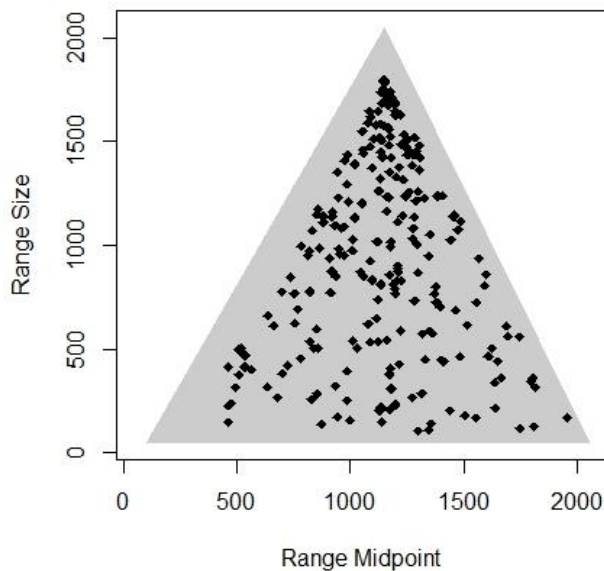


Figure 23: Mean range size as function of range midpoint for epiphytic bryophytes on the Marojejy elevational gradient.

4.3.4. Null-model predictions

All simulations under the null model yield unimodal distributions of diversity with elevation, with the predicted peaks close to those observed empirically.

For all ranges, species richness patterns largely fall within the 95% confidence interval from the null model prediction (overall species, $R^2 = 0.85$, $p < 0.001$; liverworts, $R^2 = 0.85$, $p < 0.001$; mosses, $R^2 = 0.70$, $p < 0.01$). However, empirical species richness tends to be lower than the predicted richness (Figure 24). Small ranged species (<1000 m) showed poorer fit to null models (overall species, $R^2 = 0.77$, $p < 0.001$; liverworts, $R^2 = 0.78$, $p < 0.001$; mosses, $R^2 = 0.46$, $p < 0.05$). Whereas the large ranged species (>1000 m) showed better fit to null models (total species, $R^2 = 0.88$, $p < 0.001$; liverworts, $R^2 = 0.82$, $p < 0.001$; mosses, $R^2 = 0.86$, $p < 0.001$).

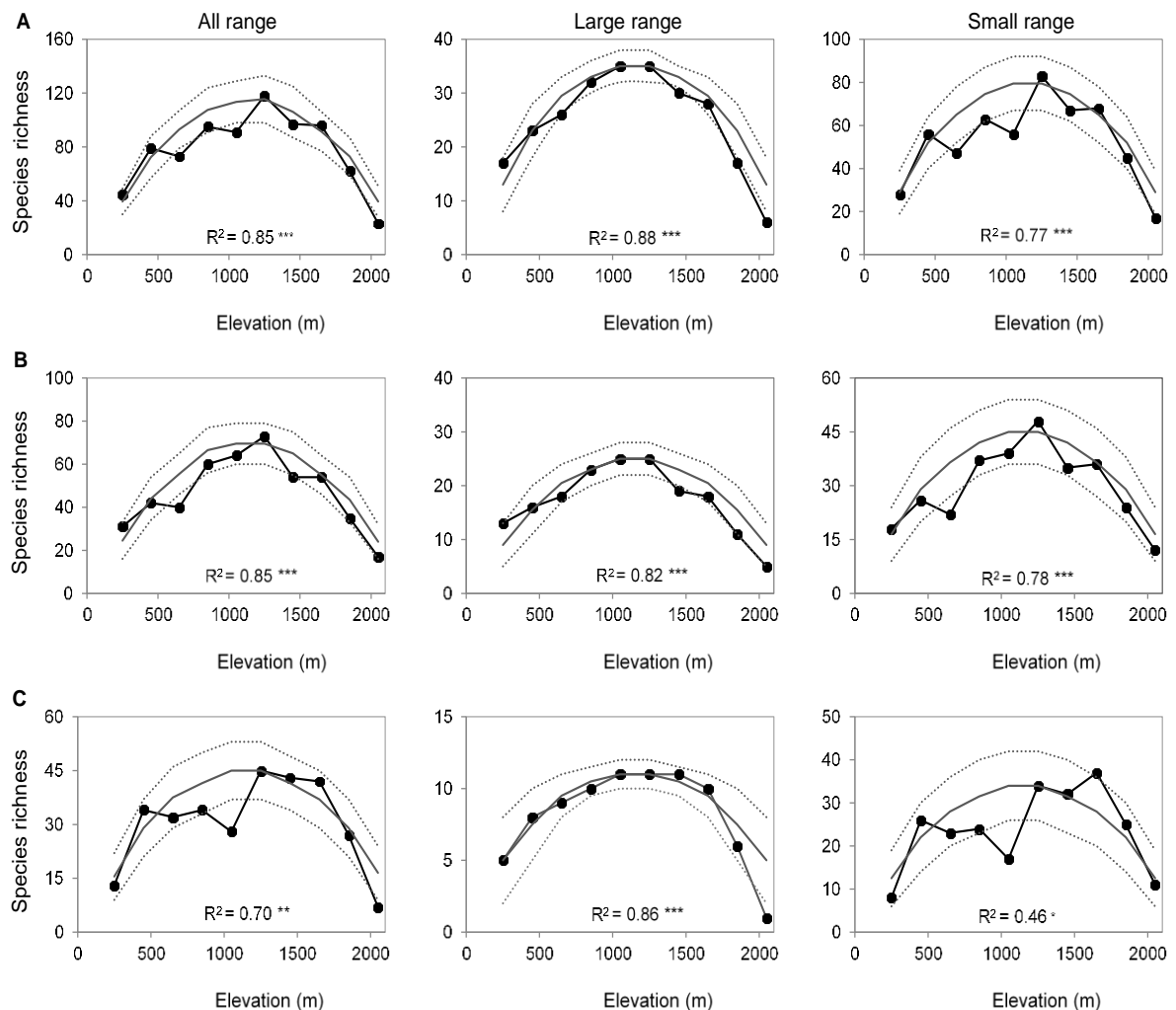


Figure 24: Null model predictions generated by a Monte Carlo procedure based on 50000 simulations (without replacement) of empirical range sizes using the mid-domain null program (McCain, 2004) for testing the mid-domain effect (MDE). (A) Overall species, (B) Liverworts, (C) Mosses. Empirical species richness (black line connecting the data point), predicted species richness (grey solid line) and upper and lower 95% confidence intervals (grey dotted lines).

4.3.5. Relationship between environmental variables and species richness pattern

Vegetation type is significantly correlated with liverworts species richness (ANOVA, $F = 8.198$, $p < 0.05$), whereas its correlation with the overall species and moss species richness patterns was weaker (ANOVA, overall species: $F = 4.441$, $p < 0.1$; mosses: $F = 1.222$, $p = 0.38$). The MDE is significantly correlated with the overall species richness and both moss and liverwort species richness (ANOVA, overall species: $F = 12.49$, $p < 0.01$; moss: $F = 7.055$, $p < 0.05$; liverwort: $F = 9.436$, $p < 0.05$).

Five variables were retained for the first GLM model (without MDE); four variables present a positive influence on the species richness; the mean temperature has negative influence for liverwort; where for moss canopy height and mean temperature have negative influences on species richness. Similarly, in the second model with MDE, mean temperature has a negative influence on the species richness for both overall species and liverworts; and both mean temperature and canopy height have negative influences on mosses (Table 6).

The GLM model without MDE indicates that for the overall species, mosses and liverworts, the mean temperature was found to be an important factor in shaping the overall species richness pattern. The model with MDE shows that canopy height only contributes significantly to the shaping species richness pattern for liverworts (Table 6) Both model show that, mean relative humidity and vapour pressure deficit contribute significantly to the shaping of mosses species richness pattern but were not significant for liverworts and the overall species. (Table 6).

Table 6: Multiple General Linear Regression (GLM) analyses of species richness against environmental variables for the overall species, mosses and liverworts. Referring to the regression coefficient of the respective variable in the model (z value)

	Overall species		Mosses		Liverworts	
Model without MDE						
	z-value	p (z)	z-value	p (z)	z-value	p (z)
vege	0.98		0.449		0.953	
cmea	1.358		-1.329		2.597	
temp.m	-3.053	**	-3.239	**	-1.728	**
rh.m	1.805	(.)	2.833	**	0.457	(.)
vpd	1.759	(.)	2.811	**	0.419	
AIC	94.58		79.62		78.92	
Model with MDE						
	z-value	p (z)	z-value	p (z)	z-value	p (z)
vege	0.794		0.348		0.922	
cmea	0.747		-1.859	(.)	2.332	*
temp.m	-1.896	(.)	-1.57		-1.475	
rh.m	1.338		1.983	*	0.432	
vpd	1.315		1.991	*	0.398	
MDE	1.324		1.909	(.)	0.024	
AIC	94.79		77.73		80.92	

vege = vegetation type, cmea = Canopy height (m), temp.m = Mean temperature (°C), rh.m = Mean relative humidity (%), vpd = Vapour Pressure Deficit (Pa), MDE = Mid domain effect, AIC = Akaike information criteria. Model fit was assessed using the AIC, smaller values of AIC indicates better fits. (.) p-value<0.1 * p-value < 0.05, ** p-value < 0.01

Canopy height was poorly correlated with species richness in the ANOVA, but significantly correlated with species richness when applying second order polynomial regressions models (Table 7). When a second order polynomial regression was applied, the canopy height regression value increased from 0.001 to 0.6478 for the overall species, 0.00005 - 0.5238 for liverworts and 0.000 to 0.5658 for mosses.

Table 7: Second order polynomial regression analysis.

	Overall species		Mosses		Liverworts	
	R^2	AIC	R^2	AIC	R^2	AIC
cmea	0.6478 *	87.23043	0.5658 *	69.37416	0.5238 (.)	80.5523
temp.m	0.3345	93.59418	0.1058	76.59792	0.3525	83.62563
rh.m	0.3099	93.95639	0.1872	75.64279	0.2854	84.61167
vpd	0.4008	92.54443	0.2285	75.12128	0.3665	83.40628
MDE	0.6268 *	87.81037	0.5829 *	68.9724	0.6381 *	77.80829

cmea = Canopy height (m), temp.m = Mean temperature (°C), rh.m = Mean relative humidity (%), vpd = Vapour Pressure Deficit (Pa), MDE = Mid domain effect, AIC = Akaike information criteria. Model fit was assessed using the AIC, smaller values of AIC indicates better fits. (.) p-value < 0.1, * p-value < 0.05

4.4. Discussion

To date, this is the first ecological study on the epiphytic bryophyte diversity and distribution patterns in Madagascar. It reveals a high diversity of epiphytic bryophytes in Marojejy National Park, and documents the elevational pattern of this diversity. As commonly found in tropical and sub-tropical elevational gradients, small ranged species contribute more to the overall species richness than large ranged species (Ah-Peng *et al.*, 2012; Henriques *et al.*, 2016). Furthermore, analyses indicate a hump-shaped pattern of species richness along the elevational gradient. This study produces evidence that bryophyte richness along the Marojejy elevational gradient was strongly explained by the null mid-domain effect, but climatic variables also play important roles in shaping richness pattern. The mid-elevation region of the National Park, with its favourable environmental conditions, facilitates higher species richness in epiphytic bryophytes than the lower and upper end of the gradient.

4.4.1. Sampling efficiency and species range interpolation

The standardised hierarchical methodology used to sample bryophyte communities was designed to obtain a large amount of data enabling assessment of the diversity and distribution of bryophytes along elevational gradients (Ah-Peng *et al.*, 2007; Gabriel, Bardat, *et al.*, 2014). It has been replicated on Comoros, La Réunion, Kenya and Madagascar, and later in a more extensive project that added transects from the Azores, Canarias, Guadeloupe, and Tahiti (Gabriel, Bardat, *et al.*, 2014). For this study, ten

elevational sites were explored. As shown by the sample-based accumulation curves (Figure 17: one at each of the ten elevational sites), this sampling method underestimated the diversity of the sampled community in these rich ecosystems. The non-parametric diversity estimators (Chao, Jackknife 1 and ACE) estimated higher values of species richness, but showed a similar distribution pattern to the observed species richness. They suggest respectively, that only 56-76%; 81-92% and 59-70% of the species richness was sampled for each elevation. According to Ah-Peng *et al.* (2012), an exhaustive sampling of species could be hard to reach biodiversity hotspots for such a diverse group of plants. The possibility that many species might have not been inventoried can not be excluded.

In most elevational gradient studies the distributional range of a species is calculated by subtracting the minimum from the maximum elevation at which the species is observed (e.g. Ah-Peng *et al.*, 2012; Henriques *et al.*, 2016). The accuracy of this interpolation method has been discussed by Grytnes & Vetaas (2002) since it may artificially increase richness at mid-elevation areas, because some species are only recorded from both ends of their elevational ranges. But there is no evidence that species cannot be found within the interpolated range, and this may not significantly affect the trend of species distribution. Only five species: *Aerobryopsis capensis* (Müll.Hal.) M. Fleisch. (450-1250 m), *Ceratolejeunea belangeriana* (Gottsche) Steph. (250-1250 m), *Ceratolejeunea calabariensis* Steph. (250-1050 m), *Cheilolejeunea surrepens* (Mitt.) E.W. Jones (250-1250 m) and *Leucoloma chrysobasilare* var. *chrysobasilare* (Müll.Hal.) A. Jaeger (450-1050 m), were recorded at the limits of the observed range but not between.

4.4.2. Species composition and richness pattern

The epiphytic bryophyte flora of Marojejy National Park is relatively rich (254 species: 157 liverworts and 97 mosses). This is comparable to ferns, for instance, where 274 species were reported from the same gradient (Rakotondrainibe, 2000). Many of the families with high species richness on Marojejy (*Lejeuneaceae*, *Dicranaceae*, *Lepidoziaceae*, *Orthotricaceae*, *Frullaniaceae*, *Sematophyllaceae*, *Plagiochilaceae*, *Calymperaceae*) are globally diverse in tropical rain forests (Gradstein & Pócs, 1989). Bryophyte endemism, on the other hand, is relatively low in comparison to other groups. The number of liverwort species recorded is higher than that of mosses at all elevations. This is often the case in tropical rain forests (Cornelissen & Ter Steege, 1989; Cornelissen & Gradstein, 1990; Gradstein *et al.*, 2001; Acebey *et al.*, 2003; Ah-Peng *et al.*, 2012). The preponderance of liverworts over mosses is generally seen as a characteristic of mid and

high elevations and epiphytic communities (Gradstein & Salazar Allen, 1992; Andrew *et al.*, 2003; Grau *et al.*, 2007). In sub-tropical islands, in contrast, higher moss species richness is often seen at lower elevations (Henriques *et al.*, 2016).

Our results showed a mid-elevation peak at 1250 m in species richness pattern of epiphytic bryophytes on the Marojejy gradient. This is consistent with previous work on vascular plants of the massif (Messmer *et al.*, 2000; Rakotondrainibe, 2000). Recent comparison by Gabriel, Bardat, *et al.*, (2014), of species richness patterns of liverworts on tropical (Madagascar and La Réunion) and subtropical (Azores and Canaries) islands, showed this pattern for all islands, although the absolute elevation where richness peaks may differ. This hump-shaped pattern is the most common pattern observed in studies of long elevational gradients (Grau *et al.*, 2007; Ah-Peng *et al.*, 2012; Spitale, 2016). The mid-elevation peak can be explained by the fact that this level is characterised by a zone of shorter, dense vegetation, forming a transition zone between montane scrub and montane forest. It is to be noted that plots at 450 m were set-up in the vicinity of Humbert's waterfall, which may explain the sudden increase in species richness at 450 m and then the drop-down of species richness at 650 m.

4.4.3. Spatial and environmental factors

The mid-domain-effect, the outcome of a stochastic geometric process, has been invoked as an explanation of hump-shaped patterns of species richness along a number of elevational gradients (Colwell *et al.*, 2004). In this study, the empirical species richness showed significant fit to the null model prediction curves, thereby indicating that the species richness patterns may be constrained by geographic hard boundaries. Moreover, MDE was more pronounced when large-ranged species (> 1000 m) were considered for the overall species, mosses and liverworts. This confirms the prediction of the MDE hypothesis that small-ranged species (<1000 m) will be less affected by the MDE than large-ranged species (Jetz & Rahbek, 2001; Colwell *et al.*, 2004; Kluge *et al.*, 2006). This is in line with the results from recent studies (e.g. Ah-Peng *et al.*, 2012; Tang *et al.*, 2014) on the pattern of species richness in continental mountain forests. However, Ah-Peng *et al.* (2012) found that the pattern on an oceanic island (La Réunion Island) was not well predicted by the MDE, due to the concentration of rare species at mid-elevation and the absence of species at highest elevation. When the correlation of species richness and individual explanatory variables was examined based on linear regression, we found that MDE is an important predictor of species richness of bryophytes. However, the highest

number of rare species (shorter range distribution) was also found at mid-elevation in the Marojejy elevational gradient. This suggests a continental trend in bryophyte richness pattern along this gradient. According to Lees *et al.* (1999) and Lees & Colwell (2007), the Mid-domain effect is well demonstrated in Madagascar with a convincing example of a broad-scale gradient of species richness, this is here reinforced for another taxon, bryophytes. However, in combination with other variables in a multiple regression model and a second order polynomial, MDE appears to be a weaker predictor (Table 6, Table 7). MDE generally excludes any evolutionary, climatic or biotic influences on species richness (Colwell *et al.*, 2004). Thus, we suspect that the influence of MDE was masked by the strength of other environmental variables in the multiple regressions.

Several environmental variables have been proposed to explain the distribution patterns of species richness along elevational gradients. The most frequently proposed include vapour pressure deficit, relative humidity, rainfall, temperature, geometric constraints, habitat heterogeneity and evolutionary history (Acebey *et al.*, 2003; McCain, 2007; Sun *et al.*, 2013; Yu *et al.*, 2013; Tang *et al.*, 2014; Szewczyk & McCain, 2016).

In this study, the set of climatic factors is limited to five variables. Temperature, relative humidity and vapour pressure deficit showed significant correlations with the richness patterns in the multiple regressions without the effect of MDE for the overall species and mosses and a weak correlation for liverworts (Table 6). More specifically, for overall species and mosses, mean temperature turned out to be the best predictor of species richness patterns. Vegetation type and canopy height were considered as habitat heterogeneity criteria. Both showed a weak correlation with the hump-shaped pattern of species richness in the ANOVA, but in the multiple regression model canopy height appears to show a strong correlation with liverwort and moss species richness (Table 6). Canopy height was found to be an important predictor of species richness in other surveys dealing with bryophytes (Wolf, 1993; Andrew *et al.*, 2003; Sun *et al.*, 2013).

These observations, therefore, support the explanation that optimum interaction of water and energy leads to higher biological productivity triggering higher species richness (Bhattarai *et al.*, 2004; Manish *et al.*, 2017). The combined effects of temperature and humidity influence species richness along elevational in three different ways. The cooler average temperatures, coupled with constant mist and cloud, are ideal environmental conditions for the growth of epiphytic bryophytes. At the lower end of the gradient, species richness is constrained by higher temperature and reduced relative humidity,

whereas at the upper end of the transect, species richness is limited by low temperature and relative humidity (Kluge & Kessler, 2006; Lee *et al.*, 2013; Tang *et al.*, 2014). The longer dry periods, the taller vegetation and an often-closed canopy might be the cause of lower species richness at lower elevations. Furthermore, the higher temperatures produce more rapid desiccation of tree trunks at lower elevations (Zotz, 1999; Bader *et al.*, 2013; Wagner *et al.*, 2013). At mid-elevation, an optimum range of temperature and relative humidity lead to maximum productive energy availability. Moreover, the presence of a cloud zone, depositing a large amount of water directly onto vegetation, reduces evapotranspiration and increases atmospheric humidity (Bruijnzeel & Veneklaas, 1998; Bhattarai *et al.*, 2004). For future studies, other possible drivers of bryophyte distribution patterns (such as light exposure or substrate pH, for example) need to be considered. The decrease in species richness at higher elevations is probably due to the open, montane scrub physiognomy, the lack of microhabitat availability, low temperature and high light intensities. In addition, at high elevations evaporation slows down (Zotz, 1999).

Surprisingly, our results highlight noticeably different responses of epiphytic liverworts and mosses to the predictor variables examined. Environmental variables drive changes in species composition of mosses and only weakly of liverworts. These differences indicate that, in contrast to Ah-Peng *et al.* (2012) and Henriques *et al.* (2016), mosses in Marojejy were more sensitive to changes in their surrounding environment. Therefore, mosses can be as good candidates as liverworts for climate change indicators in this system. Liverworts are otherwise suggested to be particularly more sensitive to microclimate changes. Despite abundant moisture in rain forest communities, they undergo repeated cycles of rapid drying and re-wetting (Proctor *et al.*, 2007). Our results suggest that canopy height and vegetation type are the main drivers of changes in species composition of liverworts. Their sensitivity to canopy height and vegetation type is also in line with Wolf (1995) on the bryophyte communities in Columbian upper montane forests.

4.4.4. Conclusions

The present study shows a hump-shaped distribution pattern of epiphytic bryophyte species richness along the Marojejy elevational gradient, with species richness peaking at 1250 m. Environmental factors and the MDE had good explanatory power and were the main potential factors determining the richness patterns of plant species. Marked differences occurred between liverworts and mosses, with relative humidity and vapour

deficit pressure together able to predict the overall and moss species richness, and vegetation type for liverworts.

Species richness along Marojejy elevational gradient is dominated by small ranged size species. Thoses species are possibly more sensitive to environmental changes than larger-ranged species. Their occurrence throughout the elevational transect suggests that conservation efforts should consider the entire gradient rather than just species-rich areas.

CHAPTER 5

Diversity partitioning and community structure of the epiphytic bryophytes of the Marojejy National Park

5. Diversity partitioning and community structure of the epiphytic bryophytes of the Marojejy National Park

5.1. Introduction

Since observations by Darwin, Wallace and Von Humboldt on the biological and ecological changes with elevation (Lomolino, 2001), the study of elevational gradients has become a central topic in ecology. Ecologists and conservation biologists have, in general increased their interest in the pattern of diversity and distribution of species along elevational gradients, largely attempting to elucidate the factors controlling these patterns. Environmental conditions and the biotic interactions within and between trophic levels that occur on mountains are key features in the control of species diversity and distribution patterns (Eisenlohr *et al.*, 2013).

Species richness and diversity change over multiple scales for a number of reasons including dispersal processes, environmental filters and niche conservatism (Maire *et al.*, 2012; Baldeck *et al.*, 2013; Gross *et al.*, 2013). Legendre & De Cáceres (2013) note that the most interesting property of species diversity is its organisation through space. Assessing the spatial variation in species composition of different communities consists of not only identifying the presence and abundance of species but also characterizing the organisation and structure of communities (Gimingham & Birse, 1957; Dai *et al.*, 2006). Understanding such organisation is an important tool in testing hypotheses about the processes that generate and maintain biodiversity in ecosystems (Legendre & De Cáceres, 2013).

The partitioning of diversity into hierarchical, scale-related components is one interesting approach to understanding the organisation of species diversity. It is a fruitful approach for analysing patterns of diversity from a multiscale hierarchical sampling concept (Crist *et al.*, 2003) and is useful in studies of conservation biology and restoration (Lande, 1996). Whittaker (1972) partitioned diversity into hierarchical scale-related components as follows: α (within-site diversity); β (diversity among sites); and γ (regional diversity). Conceptually, γ -diversity is the total diversity of a region or other spatial unit. Whilst α -diversity describes the species diversity within a sampling unit (local community or habitat), its analysis often involves comparisons of mean species richness found in a set of samples. β -diversity, expressed as species turnover rate or similarity index between communities, describes how local communities within an area or region differ in species composition and abundance. This last can, in turn, be decomposed into two additive

components accounting for spatial turnover and nestedness which result from two opposite processes (Baselga, 2010). Spatial turnover is the replacement of species from one site to another as a result of either contemporary or historical niche and dispersal processes. Nestedness, on the other hand, reflects species loss or gain due to selective extinction, selective colonization, and habitat nestedness (Podani & Schmera, 2011; Carvalho *et al.*, 2012). Nestedness-driven dissimilarity occurs when the biotas of sites with smaller numbers of species are subsets of the biotas of richer sites (Baselga, 2010, 2012). Disentangling the contribution of nestedness and species turnover to the total beta-diversity is crucial for connecting the spatial structure of species assemblages to ecological processes (Legendre *et al.*, 2005).

Epiphytic bryophytes offer an excellent model for the study of beta diversity in tropical systems for multiple reasons. They are important components of biodiversity in most humid tropical mountain forests in term of biomass and abundance, and a large number of species can be obtained from a relatively small area. They play an important role in ecosystem functioning, and services such as carbon storage and water balance, soil thermal regimes, and moisture and nutrient availability (Coxson, 1991; Gradstein, 1992; Curtis *et al.*, 2005). There are very few studies linking diversity patterns to the partitioning of diversity into its different components in epiphytic bryophyte systems (Aranda *et al.*, 2013; Henriques *et al.*, 2016). To date, no surveys of this sort have been undertaken on the bryophytes of Madagascar. Here we examine the diversity of epiphytic bryophytes along an elevational gradient in Marojejy National Park in the Sava Region of north-eastern Madagascar to answer the following questions (1) What are the contributions of alpha and beta diversity to the total gamma diversity across spatial scales, from sample to elevational band? (2) Do organisms not limited by dispersal, such as bryophytes, exhibit a specific pattern for β -diversity along the elevational gradient? (3) Do the different components of β -diversity (i.e., turnover and nestedness-resultant) possess different spatial patterns? and (4) Based on the proportions of each biodiversity component and the relative contributions of turnover and nestedness components for epiphytic bryophytes, what are the potential conservation strategies for biodiversity management?

The overarching hypothesis is that high levels of beta diversity may arise from the ecological effects of habitat heterogeneity and dispersal limitation. We also expect that additive partitioning of species richness will largely show high beta diversity whilst partitioning of Shannon and Simpson diversity will be characterised by a high alpha

diversity due to the generality in the relationship between species distribution and abundance.

5.2. Materials and Methods

5.2.1. Study area and data collection

The study was carried out in Marojejy National Park, north-eastern Madagascar. Bryophytes were collected along an elevational transect at 200 m intervals from 250 m to 2050 m (10 sites in total) using a hierarchically nested design. Sampling was undertaken at four hierarchical levels: elevational belt (every 200 m), plots (10 x 10 m), quadrats (2 x 2 m) and microhabitat (50 cm²). The epiphytic microhabitat is composed of TA (0-0.5 m), TB (0.5-1 m) and TC (1-2 m), the canopy for practical reasons was not investigated in this study. The descriptions of the study area, the sampling protocol and the environmental data collections are detailed in Chapter 4.

5.2.2. Data analyses

5.2.2.1. Sampled-based accumulation curves

A descriptive analysis was first conducted to assess how species richness in bryophyte communities varies across the four hierarchical scales included in this study. To do so, sample-based accumulation curves were used to plot the total number of species as a function of the number of samples examined, assuming that they were selected randomly among the hierarchically sampled units (Gotelli & Colwell, 2001). Samples were added to the species accumulation curve using 999 random replicates to avoid variation in the curve shape due to accumulation order that arises from sampling error and heterogeneity among the units sampled. Estimates of species richness are assumed to be accurate if the species accumulation curve reaches a plateau. The “rarefaction” method based on the output of the R function *specaccum* from the package *vegan* (Oksanen *et al.*, 2015) was applied.

5.2.2.2. Additive partitioning and hierarchical analyses of biodiversity

Any diversity measurement can be additively partitioned if the overall species diversity is equal or greater than the average diversity within communities (Lande, 1996). If γ is the total diversity found in a collection of sampling units, α is the average diversity within the sampling units and β is the diversity among sampling units, γ can be partitioned into the average diversity within and among samples, so $\gamma = \alpha + \beta$ (Lande, 1996). Diversity partitioning used here follows the methods of Crist *et al.* (2003), by extending the additive procedure across multiple scales. Therefore α -diversity in this study consisted of species richness per microplots (α_1), quadrat (α_2), plot (α_3), and elevation belt (α_4). β -

diversity indicates differences in species composition among samples within each hierarchical level.

Diversity can be partitioned additively as: $\gamma = \alpha_1 + \sum_{i=1}^m \beta_i$ where i is the level of sampling in a hierarchical sampling design, $i=1$ represents the smallest sampling unit and m the highest sampling level. The formula of Crist *et al.* (2003) can therefore be reformulated as $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3 + \beta_4$ where α_1 and β_1 represent the alpha and beta diversity in the microplot level, β_2 , β_3 and β_4 represent beta diversity in the three subsequent levels: quadrat, plot, and elevational belt.

Species richness index was used to account for the pure effects of the number of species, and the Simpson and Shannon indices were used to account for the combined effects of species and their abundances. The Simpson index is weighted towards common species, whereas the Shannon index is weighted equally towards rare and common species (Magurran, 1988). For an average diversity, $\alpha_i = \sum_{j=1}^{n_i} D_{ij} q_{ij}$ where q_{ij} are the sample weights determined by the proportion of the total number of individuals found in each sample j . The Shannon index D_{ij} , is calculated as $-\sum_k p_{ijk} \ln p_{ijk}$ where p_{ijk} is the proportional abundance of species k in each sample j . Simpson's index is obtained as $1 - \sum_k p_{ijk}^2$.

To see if there are different patterns of diversity partitioning among bryophyte groups and communities, the total number of species, liverworts and mosses were evaluated separately, and diversity components were separately analysed within each microhabitat and elevation.

Individual-based randomizations, using a reshuffling algorithm, were used to test whether the observed partitioning of diversity at all hierarchical levels could have been obtained by a random distribution of individuals among samples. This was done by the “r2dtable” null model method, described in Patefield (1981). Individual-based randomizations were repeated 999 times. The additive partitioning was computed using the “adipart” function of the Vegan Package (Oksanen *et al.*, 2015) in R software (R Core Team, 2015).

5.2.2.3. Partitioning beta diversity into richness and turnover components

The total beta diversity refers to all compositional changes between two sites irrespective of the process that originated it (Whittaker, 1972). Numerous methods have been proposed to disentangle the effects of richness and replacement on overall beta-diversity (Baselga, 2010; Podani & Schmera, 2011; Carvalho *et al.*, 2012). Almeida-Neto

et al. (2011) suggest that, in the absence of nestedness, Balsega’s method (2010) is not a true measure of between sites dissimilarity due to nestedness. Baselga’s (2012) review has demonstrated that Podani & Schmera (2011) and Carvalho *et al.* (2012) approaches also have problems, since their β_{repl} (turnover) overestimates the fraction of total dissimilarity that can be attributable to richness differences (β_{rich}). Subsequently, Baselga & Orme (2012) have proposed a means of decomposing beta diversity into its turnover and nestedness components that accounts for these problems. This is used for the present study.

Total beta diversity can be measured as the Sørensen dissimilarity between two communities (β_{SOR}). First, we used a multiple-site dissimilarity measure to compute the overall beta diversity of bryophyte communities among sites following Baselga & Orme (2012). This method partitions the total Sørensen dissimilarity (beta diversity, β_{SOR}) into its dissimilarity components due to species replacement (β_{SIM} , i.e. turnover) and nestedness (β_{SNE} , i.e. richness difference)

For two sites A and B, if a is the number of shared species, b and c are the species exclusive to each site $\beta_{\text{SOR}} = \frac{b+c}{2a+b+c}$. The Simpson dissimilarity index describes species turnover without the influence of richness gradients, i.e. when one species is replaced by another species from one site to another. β_{SIM} is expressed as $\frac{\min(b,c)}{a+\min(b,c)}$. In the absence of nestedness, β_{SOR} and β_{SIM} are equal. Therefore, β_{SNE} is expressed as $\beta_{\text{SOR}} - \beta_{\text{SIM}} = \frac{|b-c|}{2a+b+c} \times \frac{a}{a+\min(b,c)}$.

This decomposition was computed using the “beta.multi” function of the betapart Package (Baselga *et al.*, 2017) in the R software (R Core Team, 2015).

5.2.2.4. Site classification and environmental factors

As a second measure of regional beta diversity, we constructed the pairwise dissimilarity matrices for each of the three beta diversity measures ($\beta_{\text{pair-sor}}$, $\beta_{\text{pair-sim}}$ and $\beta_{\text{pair-sne}}$) to identify the sites with higher species turnover. A hierarchical agglomerative cluster analysis using Ward’s linkage method was performed on the generated species turnover matrix. Pairwise dissimilarity and clustering analyses were computed using the “hclust” and “beta.pair” function of the vegan and betapart Package (Baselga *et al.*, 2017) in R (R Core Team, 2015).

To determine which environmental and spatial factors best explain the $\beta_{\text{pair-sor}}$, $\beta_{\text{pair-sim}}$ and $\beta_{\text{pair-sne}}$ patterns, we perform a multivariate ANOVA of epiphytic

bryophytes communities, based on dissimilarity, using the function *adonis* of the Vegan package (Oksanen *et al.*, 2015).

5.3. Results

5.3.1. Sample-based accumulation curves

A total of 254 species, comprising 157 liverworts and 97 mosses, distributed in 39 families and 85 genera were collected from the Marojejy elevational gradient. The sample-based accumulation curves indicate that at no hierarchical level was an asymptote reached. However, the number of species increased much faster at the microhabitat sampling level, where the curve is the closest to reaching an asymptote (Figure 25).

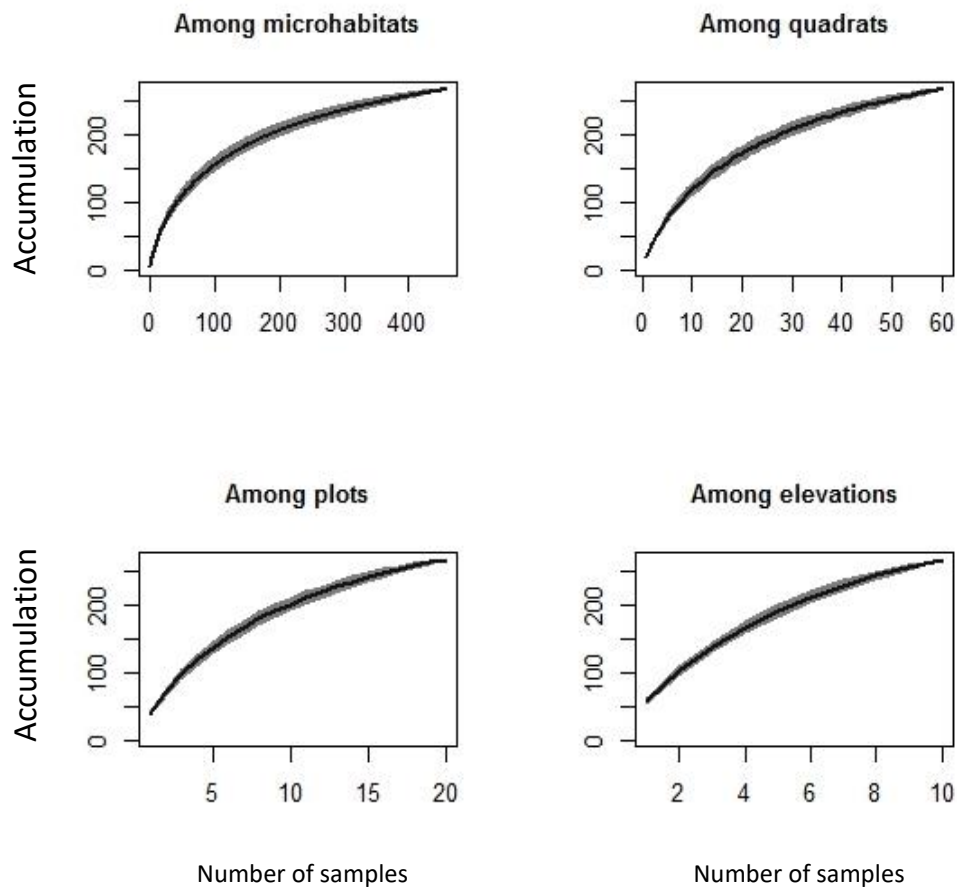


Figure 25: Species accumulation curves showing the total number of species in a given number of plots, among microhabitats (50 cm²), quadrats (4 m²), plots (100 m²) and elevations (every 200 m). The thick lines show means and the shaded regions the standard deviation ranges.

5.3.2. Additive partitioning of bryophyte diversity

Along the Marojejy elevational gradient, hierarchical partitioning reveals that at the highest level (among elevational belts), beta diversity β_4 (species richness) was a dominant trend. Regardless of the microhabitat or taxonomical group, the variation in species richness across the whole transect is largely attributable to differences among elevational belts. The lowest richness is observed at the lowest hierarchical level: α_1 within microplots, β_1 among microhabitats. α_1 contributes less than 4% of the species richness, and β_1 less than 8% (Figure 26).

In contrast, 70 to 80% of the diversity was attributable to α_1 when computed with the Simpson's index, and the proportion of diversity decreases with an increasing scale. Mosses are an exception with α_1 and β_1 representing, respectively, 54% and 31% of the diversity. When diversity partitioning was computed using the Shannon's index, the observed pattern was intermediate between the other two: α_1 comprises 38-39% of the diversity, except for mosses where it represents only 22%, β_1 is the second most important proportion of diversity. Diversity was lowest at the among-plot (β_3) scale for both Shannon and Simpson indices (Figure 26).

The same patterns of diversity partitioning are observed when the data from each elevation were considered separately (Figure 27), where the lowest diversity was observed within microplots for all elevations when expressed as species richness. However, when expressed as either Shannon's and Simpson's index, the highest diversity is observed within microplots and β_2 and β_3 represent the smallest proportion of diversity.

Comparisons of the observed and expected diversity from the null model, revealed that most levels deviated from those expected under the null distribution (value from 999 randomizations, Table 8). For all groups, observed diversity within microplots (α_1) and among elevational belts (β_4) is significantly higher ($p < 0.001$) than expected under the null hypothesis for all three measures. The same patterns are observed for both mosses and liverworts and for each of the three studied epiphytic microhabitats, where the observed α_1 and β_4 are significantly higher than expected ($p < 0.001$) for all three diversity measures. On the other hand, observed beta diversities among microplots, quadrats and plots (respectively β_1 , β_2 and β_3) expressed by the species richness, Shannon's and Simpson's diversity index were lower than expected under the null distribution ($p < 0.001$). However, the observed α_1 (TC), β_2 (TC) and β_3 (TA, TB, TC), expressed by Simpson's diversity were not significantly different from those expected by chance.

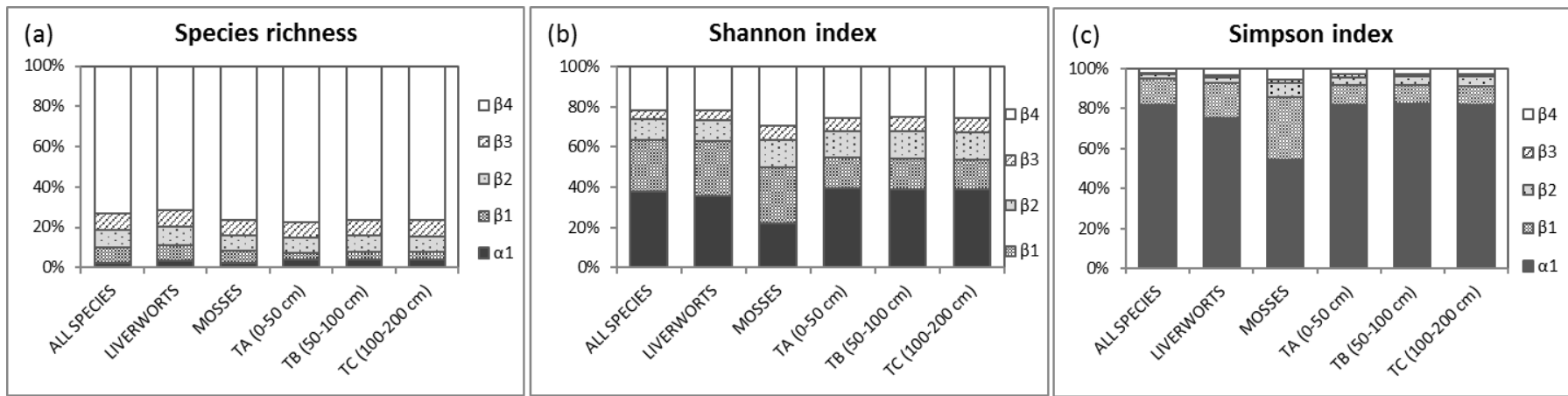


Figure 26: Additive diversity partitioning of (a) species richness, (b) the Shannon index of diversity and (c) the Simpson index of diversity into diversity components across sampling scales: α_1 (microplots), β_1 (microplots), β_2 (quadrats), β_3 (plots) and β_4 (elevations). Values are expressed as the percent of the total diversity of epiphytic bryophytes explained by each hierarchical level, for all species, Mosses, Liverworts, TA, TB and TC.

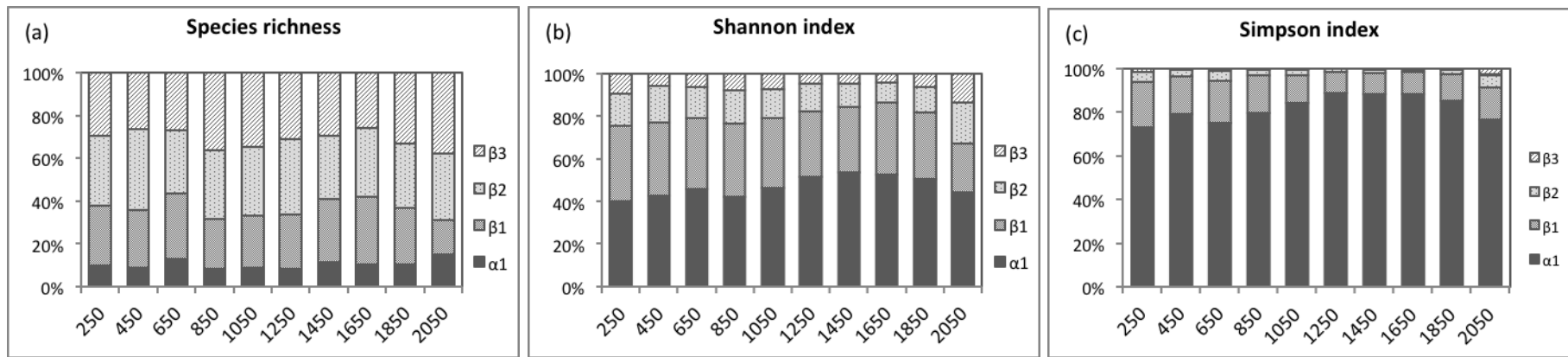


Figure 27: Additive diversity partitioning of species richness (a), the Shannon index of diversity (b) and the Simpson index of diversity (c) into diversity components across sampling scales at each elevation: α_1 (microplots), β_1 (microplots), β_2 (quadrat) and β_3 (plots) for all epiphytic bryophytes.

Table 8: Comparisons of observed (Obs) and expected (Exp) diversity from the null model based on 999 randomizations on species richness, the Shannon index and the Simpson's index of diversity. α_1 (microplots), β_1 (microplots), β_2 (quadrat), β_3 (plots) and β_4 (elevations). * p -value = 0.05, ** p -value = 0.01, *** p -value=0.001, ns not significant.

		Richness			Shannon's			Simpson's		
		Obs	Exp	p	Obs	Exp	p	Obs	Exp	p
All species	α_1	6.900	6.623	***	1.812	1.767	***	0.81	0.780	***
	β_1	19.652	30.524	***	1.204	1.687	***	0.13	0.162	***
	β_2	23.519	38.650	***	0.485	0.614	***	0.022	0.016	***
	β_3	22.044	35.461	***	0.224	0.271	***	0.006	0.004	***
	β_4	194.885	155.743	***	1.030	0.415	***	0.022	0.004	***
Liverworts	α_1	4.995	4.699	***	1.487	1.420	***	0.736	0.717	***
	β_1	12.683	19.353	***	1.125	1.581	***	0.169	0.221	***
	β_2	14.317	22.800	***	0.430	0.554	***	0.028	0.024	***
	β_3	13.148	20.164	***	0.196	0.236	***	0.008	0.006	***
	β_4	112.857	90.985	***	0.915	0.361	***	0.033	0.005	***
Mosses	α_1	2.849	2.759	***	0.908	0.875	***	0.529	0.516	***
	β_1	7.084	11.837	***	1.142	1.656	***	0.306	0.388	***
	β_2	9.546	16.703	***	0.572	0.709	***	0.066	0.047	***
	β_3	8.995	16.802	***	0.275	0.342	***	0.020	0.012	***
	β_4	92.526	72.899	***	1.224	0.539	***	0.052	0.011	***
TA (0-50 cm)	α_1	6.623	6.282	***	1.787	1.726	***	0.807	0.794	***
	β_1	6.758	8.806	***	0.681	0.889	***	0.095	0.123	***
	β_2	13.658	19.920	***	0.597	0.802	***	0.040	0.045	***
	β_3	12.693	20.861	***	0.285	0.401	***	0.012	0.011	ns
	β_4	139.268	123.131	***	1.170	0.702	***	0.029	0.010	***
TB (50-100 cm)	α_1	6.766	6.441	***	1.804	1.749	***	0.811	0.799	***
	β_1	7.196	9.055	***	0.697	0.879	***	0.094	0.117	***
	β_2	14.316	20.441	***	0.632	0.816	***	0.041	0.045	***
	β_3	14.362	21.648	***	0.309	0.415	***	0.011	0.012	ns
	β_4	137.360	122.415	***	1.165	0.748	***	0.028	0.010	***
TC (100-200 cm)	α_1	7.347	7.170	*	1.847	1.825	*	0.807	0.806	ns
	β_1	7.528	9.380	***	0.686	0.855	***	0.093	0.114	***
	β_2	15.725	22.148	***	0.647	0.827	***	0.045	0.045	ns
	β_3	16.113	23.708	***	0.330	0.428	***	0.013	0.011	ns
	β_4	151.289	135.595	***	1.209	0.785	***	0.028	0.010	***

5.3.3. Effect of nestedness and species turnover on the total diversity

Across all data partitions, (i.e. total species, mosses, liverworts, TA (0-50 cm), TB (50-100 cm) and TC (100-200 cm), the multiple-site Sørensen dissimilarity index β_{SOR} ranges from 0.90 to 0.92. We found that β_{SIM} (species turnover) accounts, by far, for the largest fraction of the overall dissimilarity (Figure 28).

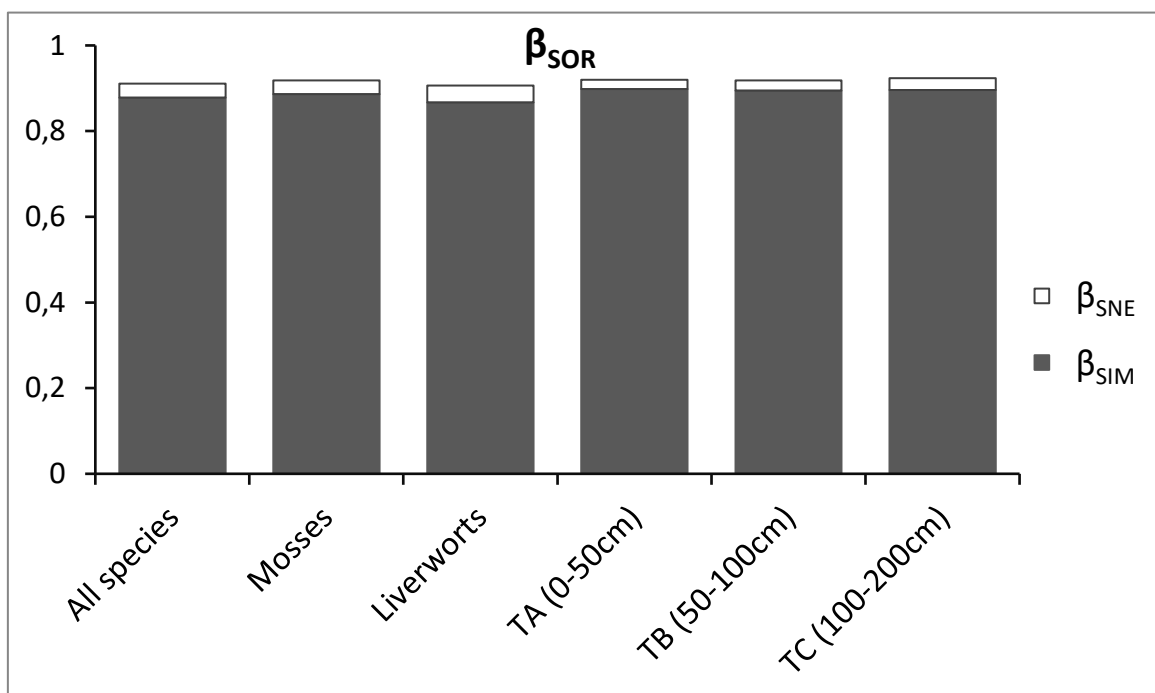


Figure 28: Partition of the multiple-site Sørensen dissimilarity (β_{SOR}) onto its components of turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) similarity for the Marojejy elevational gradient. The y axis represents the total value of β_{SOR} .

The overall dissimilarity (β_{SOR}) is higher for mosses than either all species combined or liverworts. β_{SOR} was also higher for TC compared to the other two microhabitats. Species turnover, β_{SIM} , is higher for mosses than for liverworts, while species nestedness β_{SNE} is higher for liverworts than for mosses. When the patterns of species turnover and nestedness-resultant dissimilarity are compared between microhabitats, TA (0-50 cm) shows the highest β_{SIM} while β_{SNE} is higher for TC (100-200 cm) than the other two microhabitats (Figure 29).

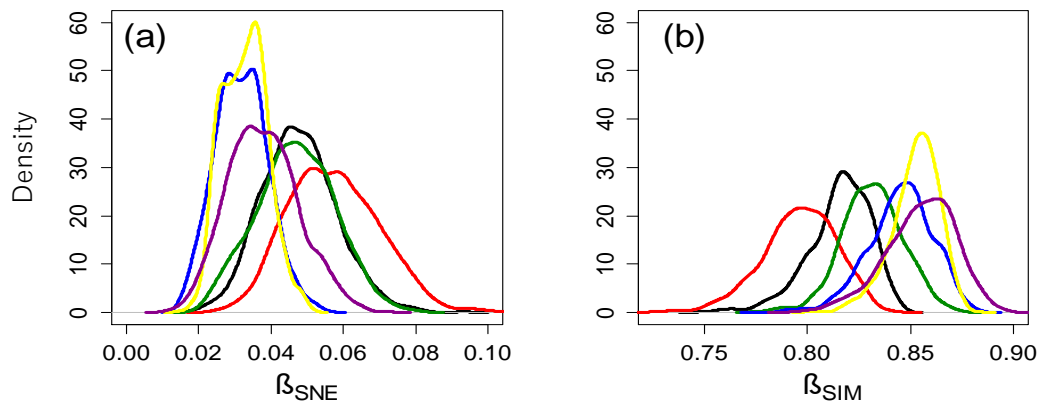


Figure 29: Density plots representing the distribution of (a) nestedness-resultant (β_{SNE}) and (b) the turnover (β_{SIM}) across 1000 samples. Multiple-site dissimilarity was computed for potential species composition for all taxonomic groups combined (black) in liverworts (red), mosses (green) and for the three studied microhabitat TA: 0-50 cm (blue), TB: 50-100 cm (yellow) and TC: 100-200 cm (purple).

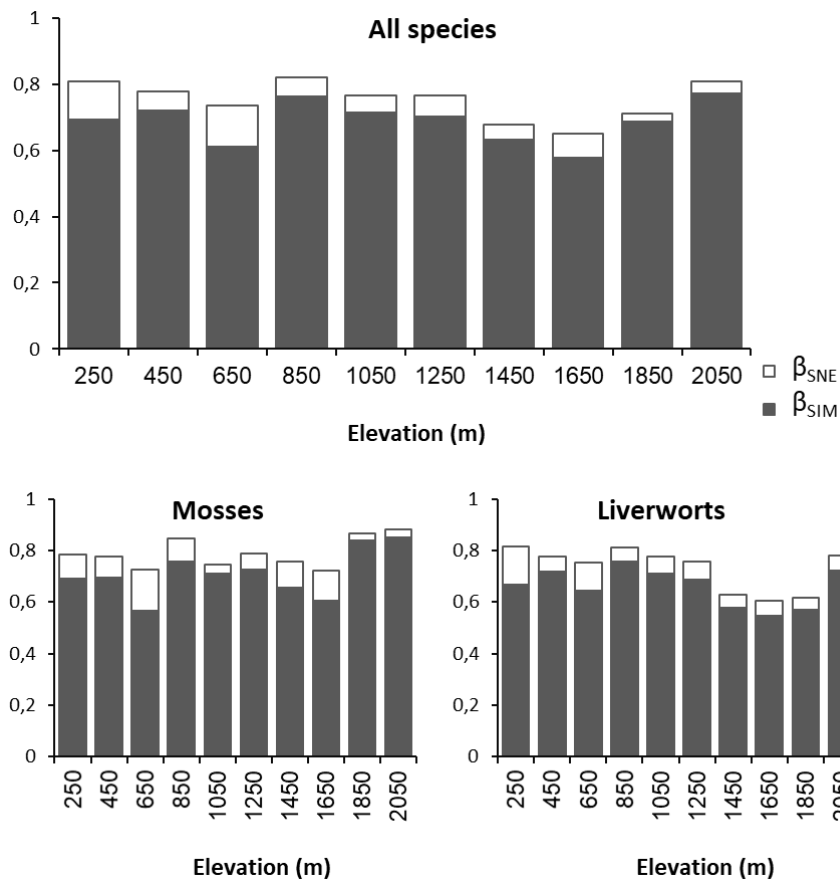


Figure 30: Partitioning of the multiple-site Sørensen dissimilarity (β_{SOR}) onto its components of turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) at each studied elevation for All Species, Mosses and Liverworts

Concerning the elevational patterns of overall dissimilarity β_{SOR} , we found that species turnover is the main driver of beta diversity across all data partitions and among bryophyte groups. There is no obvious increase or decrease of overall beta diversity along the elevational gradient. The overall dissimilarity β_{SOR} ranges from 0.65 to 0.82, where the peak occurs at 850 m and the lowest at 1650 m. Among liverworts β_{SOR} from 1450 to 1850 m sites are notably lower than the rest of the gradient. For mosses, the standout β_{SOR} values are the two highest elevations. When exploring the patterns of each one of the two processes along the elevational gradient, there is no obvious pattern with increasing elevation (Figure 30).

5.3.4. Pairwise dissimilarity among plots

Site clustering analysis derived from Sørensen dissimilarity produced two noticeable groups. There is a distinct difference in species composition between the low-elevation (up to 1050) and the high-elevation plots. This suggests that these two sets share a small number of species (Figure 31).

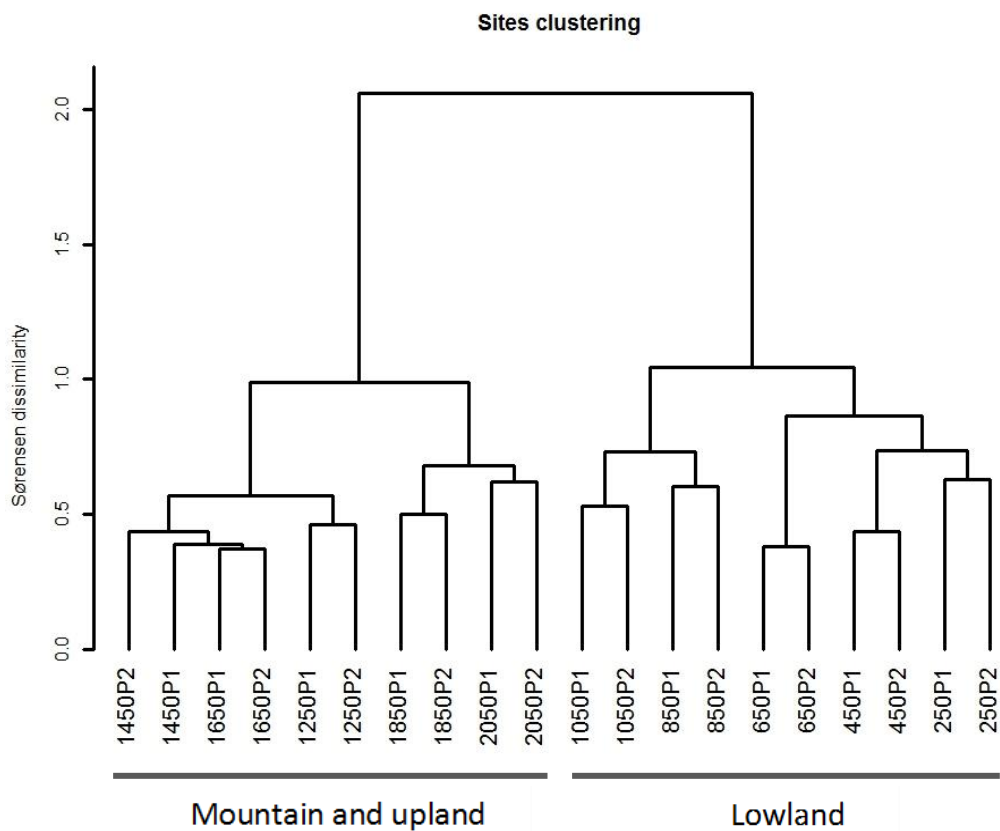


Figure 31: Among-elevation bryophyte species turnover at Marojejy National Park. Cluster analysis derived from the Sorensen dissimilarity $\beta_{\text{pair-sor}}$.

Results from the multivariate ANOVA based on dissimilarity are presented in [Table 9](#) and [Table 10](#). Assemblage similarity ($\beta_{\text{pair-SOR}}$) was significantly related to the altitude ($R^2 = 0.201$, $p < 0.001$), the Vapour Pressure Deficit ($R^2 = 0.14055$, $p < 0.001$) and vegetation type ($R^2 = 0.11883$, $p < 0.01$), when all taxonomical group are considered. The fit was much stronger for liverworts than mosses. For all three studied microhabitats, $\beta_{\text{pair-SOR}}$ was significantly related to the altitude (TA: $R^2 = 0.1975$, $p < 0.001$, TB: $R^2 = 0.21482$, $p < 0.001$ and TC: $R^2 = 0.16532$, $p < 0.001$) and the Vapour Pressure Deficit (TA: $R^2 = 0.13936$, $p < 0.01$, TB: $R^2 = 0.15167$, $p < 0.01$ and TC: $R^2 = 0.13663$, $p < 0.01$).

Table 9: Results of multivariate ANOVA based on the pairwise Sørensen dissimilarity between two communities $\beta_{\text{pair-SOR}}$ with 999 simulations.

	All species		Mosses		Liverworts		TA (0-50 cm)		TB (50-100 cm)		TC (100-200 cm)	
	<i>F</i>	<i>R</i> ²	<i>F</i>	<i>R</i> ²	<i>F</i>	<i>R</i> ²	<i>F</i>	<i>R</i> ²	<i>F</i>	<i>R</i> ²	<i>F</i>	<i>R</i> ²
alti	7.241	0.20143***	6.279	0.20419***	7.6704	0.19671***	6.7073	0.1975***	6.5829	0.21482***	4.627	0.16532***
vege	4.2716	0.11883**	2.6827	0.08724*	5.3874	0.13816**	3.977	0.11711**	2.3611	0.07705*	1.9544	0.06983*
cmea	1.4653	0.04076	0.9203	0.02993	1.8243	0.04678	1.2706	0.03741	2.1396	0.06982*	2.8224	0.10085**
temp.m	2.6888	0.0748*	2.1961	0.07142*	2.9765	0.07633*	2.3438	0.06902*	1.8474	0.06029(.)	1.8711	0.06685*
rh.m	2.2288	0.062*	2.2785	0.0741*	1.9539	0.05011	1.9289	0.0568(.)	2.0646	0.06738*	1.8887	0.06749*
vpd	5.0527	0.14055***	3.3937	0.11036**	6.1803	0.1585***	4.7327	0.13936**	4.6476	0.15167**	3.8239	0.13663**

alti = Altitude, vege = vegetation type, cmea = Canopy height (m), temp.m = Mean temperature (°C), rh.m = Mean relative humidity (%), vpd = Vapour Pressure Deficit (Pa), Magnitude of *F*.Model and *R*² indicate better fits, *** p-value < 0.001, ** p-value < 0.01, * p-value < 0.05, (.) p-value < 0.1

Table 10: Results of multivariate ANOVA based on the pairwise Sørensen dissimilarity between two communities $\beta_{\text{pair-sim}}$ and $\beta_{\text{pair-sne}}$ with 999 simulations.

	All species		Mosses		Liverworts		TA (0-50 cm)		TB (50-100 cm)		TC (100-200 cm)	
	F	R ²	F	R ²	F	R ²	F	R ²	F	R ²	F	R ²
$\beta_{\text{pair-sim}}$												
alti	9.6267	0.22962***	8.474	0.24306***	10.9751	0.22243***	8.1931	0.21458**	9.2467	0.2455***	5.907	0.19645***
vege	6.1569	0.14686**	3.7423	0.10734*	8.9718	0.18183***	5.0965	0.13348**	2.4492	0.06503*	1.3372	0.04447
cmea	1.7217	0.04107	0.5787	0.0166	2.3476	0.04758(.)	1.3619	0.03567	3.117	0.08276*	3.4077	0.11333**
temp.m	1.5137	0.03611	2.2281	0.06391(.)	1.6197	0.03283	2.3787	0.0623(.)	2.4465	0.06495*	1.5229	0.05065
rh.m	2.5548	0.06094.	1.8004	0.05164	2.8018	0.05679(.)	1.8769	0.04916	2.8412	0.07543*	2.077	0.06907(.)
vpd	7.351	0.17534**	5.0398	0.14456***	9.6247	0.19507***	6.2742	0.16433***	6.5642	0.17428***	4.8168	0.16019**
$\beta_{\text{pair-sne}}$												
alti	-0.6964	0.02538	-3.2394	-0.16938	-0.0855	-0.00404	-1.5661	-0.13166	-1.43871	-0.20348	-5.8957	-0.3171
vege	-3.0267	-0.11032	-0.078	-0.00408	-4.6938	-0.22152	-0.7615	-0.06402	2.90573	0.41096	10.2193	0.54964.
cmea	2.4093	0.08781	4.7418	0.24793	-0.0096	-0.00045	1.0628	0.08935	-2.16428	-0.30609	-1.33	-0.07154
temp.m	18.0591	0.65822*	3.9827	0.20824	14.1729	0.66889*	1.705	0.14334	-1.46319	-0.20694	5.6181	0.30217
rh.m	2.494	0.0909	7.566	0.3956	-0.3094	-0.0146	3.1056	0.26109	-0.68976	-0.09755	1.5079	0.0811
vpd	-4.8029	-0.17505	-6.8478	-0.35805	-0.886	-0.04181	-4.651	-0.39101	-1.07912	-0.15262	-2.5269	-0.13591

alti = Altitude, vege= vegetation type, cmea = Canopy height (m), temp.m = Mean temperature (°C), rh.m = Mean relative humidity (%), vpd = Vapour Pressure Deficit (Pa), Magnitude of F.Model and R² indicate better fits, *** p-value < 0.001, ** p-value < 0.01, * p-value < 0.05, (.) p-value < 0.1

5.4. Discussion

These results highlight that (1) the variation in species richness across the whole transect is largely attributable to differences among elevational belts, (2) “species spatial turnover” due to species replacement contributes most to the overall beta diversity rather than the “species nestedness” beta diversity due to species richness differences, and (3) there is a distinct difference in species composition between the low-elevation (up to 1050 m) and the high-elevation plots.

5.4.1. Small sample size can affect completeness of sampling for epiphytic bryophytes

Bryophytes were sampled across four hierarchical sampling levels: 10 elevational belts, 2 plots per elevation (20 plots), 3 quadrats per plot (60 quadrats) and 9 microplots per quadrat when available (3 samples of TA, TB and TC). A total of 457 microplots of 50 cm² were sampled during this study (Chapter 4) with species richness ranging from 1 to 31 species per microplot. This can explain why the sample-based accumulation curve for the microplots is closest to reaching an asymptote. As expected in the tropics, no asymptote was reached for the sample-based accumulation curves, due to high number of rare species and high species diversity. For such an inventory, sampling at quadrat (60 quadrats), plot (20 plots) and elevation (10 sites) levels might be not large enough.

5.4.2. Additive partitioning of biodiversity

Beta diversity at the largest sampling scale is found to be the most important contributor to the total diversity in most studies (Gering *et al.*, 2003; Summerville & Crist, 2004; Rodriguez-Zaragoza *et al.*, 2011; Acosta-González *et al.*, 2013; Gabriel, Bardat, *et al.*, 2014). Here, regardless of the microhabitat or taxonomical group considered, the lowest hierarchical level, i.e. within and between microhabitats (α_1 and β_1) contributes poorly to the total diversity, whilst, β_4 (between elevations) explained by far the greatest proportion of total diversity. The same pattern of diversity partitioning is observed when each elevation was analysed separately, where beta-diversity at the higher scales (β_3 between plots) constitutes the largest proportion of diversity. This pattern can be explained by (1) the fact that the plots at each elevation were selected in the same type of forest, so the largest variation in bryophyte species richness is produced by differences in elevation, that are necessarily related with higher habitat heterogeneity across elevations and (2) the rather homogeneous environmental conditions and/or good species movements between sample units within the different positions.

Low species richness at microplot level could be a sampling effect (Small & McCarty, 2002; Chandy *et al.*, 2006). Since species turnover contributes the most to the proportion of the overall diversity at the largest scale (β_4 , elevation), differences among elevations are very important for capturing more species. This large variation in bryophyte species richness could be related to habitat heterogeneity. Habitat heterogeneity contributes to the increase of species richness and species rarity by increasing the number of ecological niches.

As expected, the partitioning among hierarchical levels differed for the three diversity metrics as they quantify different aspects of community structure (Magurran, 1988; Gering *et al.*, 2003). This suggests that different processes affect biodiversity (species richness and abundance) at different scales (Lande, 1996; Crist *et al.*, 2003; Summerville *et al.*, 2003; Chandy *et al.*, 2006). Additive partitioning was very dependent on the microplot scale (α_1) when computed with the Simpson's and Shannon's indices, indicating higher species evenness at this scale (Gering *et al.*, 2003; Rodriguez-Zaragoza *et al.*, 2011), mainly due to the small variation in the distribution and abundance of dominant species among samples (Wagner *et al.*, 2000; Crist *et al.*, 2003; Summerville & Crist, 2004). Shannon's index was proportionally higher than Simpson's index at quadrat, plot and elevation scales, indicating an uneven distribution of the most common species at those scales. Simpson's index is more sensitive to changes in the abundance of common species than Shannon's index (Magurran, 1988; Gering *et al.*, 2003), whilst the latter is sensitive to rare species (Peet, 1974).

When tested against null models, the average α_1 (within microplots) was always significantly higher than would be expected if species distributions were determined by chance alone in all cases and β -diversities among microplots were lower than expected. This means that the two microplots at the same position are relatively similar. The higher than expected values of α_1 , indicates also rather homogeneous environmental conditions and/or effective species movement between sample units within the different positions raising the α -diversity and reducing the β -component. This is in line with the results from Luís *et al.* (2010) on riparian bryophyte communities on Madeira. The values obtained for β_1 , β_2 and β_3 for species richness are significantly lower than expected by chance, meaning that bryophyte communities are more homogeneous than those produced under the null model. This indicates that bryophyte species within each level are a subsample of the same species pool. Significantly higher beta diversity among elevations (β_4) than

expected by chance indicates that bryophyte communities are not randomly distributed along elevations.

5.4.3. Turnover and nestedness in species composition

High levels of beta diversity are often attributed to habitat heterogeneity and habitat selection (Whittaker, 1972). However, Myers *et al.* (2013) have shown that high beta diversity can also be the result of dispersal limitation. When beta-diversity was measured separately for mosses and liverworts, overall beta-diversity (β_{SOR}) was higher for mosses than for liverworts. This demonstrates that there should be more generalist species of mosses than of liverworts. Therefore, despite the small differences between liverworts β_{SOR} and mosses β_{SOR} , more species of mosses have larger distributional ranges than do liverwort species.

Multiple-site dissimilarity measurements were performed separately for the three studied microhabitats (TA, TB, TC). Above 100 cm, bryophyte communities and habitats were more homogeneous. When measured separately at each elevation, overall beta diversity β_{SOR} was highest at 850 m, meaning that species found at 850 m are mostly large ranged species (Chapter 4). The lowest value of β_{SOR} is at 1650 m for liverworts and all species considered together, whereas for mosses it is at 1050 m. This reflects a high similarity between microhabitats at 1050 m for mosses and at 1650 m for liverworts (Koleff *et al.*, 2003).

One of the most fundamental and recurrent challenges in beta diversity studies has been distinguishing and quantifying the pure “spatial turnover” component of beta diversity from that caused by variation in species richness between local communities or “nestedness” (Baselga, 2010). Very few studies have examined beta-diversity patterns of bryophytes or attempted to correlate those patterns with environmental predictors (Aranda *et al.*, 2014). Here, tests were performed to explain the contribution of the “species spatial turnover” due to species replacement (β_{SIM}) and the “species nestedness” due to species richness differences (β_{SNE}) to the overall beta diversity (β_{SOR}). As shown by partitioning the multiple-site Sørensen dissimilarity, regardless of taxonomical group (liverworts or mosses) or microhabitat (Figure 28) and at each elevation, the species turnover component (β_{SIM}) was the largest fraction of the overall bryophyte beta diversity along the elevational gradient. Besides, species turnover for all species and mosses was greater at highest elevation. The nestedness component on the other hand was highest at lower elevation (Figure 30). Habitat diversity driven by contrasting topography and environmental

variation along the elevational gradient plays an important role in generating this pattern (Carvalho *et al.*, 2012).

5.4.4. Vapour pressure deficit, relative humidity and bryophyte community assembly

The assemblage of bryophyte communities in the Marojejy massif can be relatively well predicted by climatic conditions. Water availability is well-known to be an important component of several key eco-physiological processes in bryophytes (Proctor, 1990; Zotz *et al.*, 1997). For well-established bryophyte populations, water availability at suitable temperatures for growth allows them to achieve a positive net photosynthetic rate. Hence, primarily water availability and secondarily temperature play important role in maintaining bryophytes populations and therefore ultimately in reducing the risk of species extinctions. It follows that this could justify the relevance of the considered climatic variables in this study. Given their small size, rainfall frequency, rather than the quantity of rainfall, may control bryophyte survival. In agreement with this idea, our results show that vapour pressure deficit and relative humidity correlate the most with higher values of bryophyte diversity.

5.4.5. Vegetation stage and composition of the bryoflora of the Marojejy National Park

The cluster analysis shows a distinct difference in species composition between the lower (250-1050 m) and upper (1250-2050 m) halves of the elevational gradient. Four principal vegetation types recognized, on the Marojejy massif are Montane Scrub (> 1800), Montane cloud forest (1400-1800 m), Medium-altitude Rainforest (800-1400 m), and Lowland evergreen Rainforest (< 800 m) (Goodman, 2000b). Unlike the pattern of distribution of ferns along the same gradient (Rakotondrainibe, 2000), the elevational zones occupied by bryophytes cannot be related to those of the vegetation types previously described on the massif. Considering the site cluster analysis derived from Sørensen dissimilarity values, the elevational zonation for bryophytes on the Marojejy massif should be as follows (Figure 31): (1) Lowland evergreen Rainforest (< 800 m) (2) Medium-altitude Rainforest (800-1200 m), (3) Montane cloud forest (1200-1800 m) and (4) Montane Scrub (> 1800). This zonation coincides with Faramalala's (1988) classification of the vegetation of the Marojejy massif based on the floristic composition and structure of the forest.

CHAPTER 6

A trait-based approach to assessing functional responses of epiphytic liverworts to environmental gradients

6. A trait-based approach to assessing functional responses of epiphytic liverworts to environmental gradients

6.1. Introduction

Assessing the relationship between ecosystem functioning and biodiversity has grown rapidly in the past decade (Díaz *et al.*, 2007; Song *et al.*, 2014). Assessing species responses to change in their environment and the effect of biotic interactions in shaping communities, are important steps in understanding ecosystem functioning and have potentially important consequences for conservation (Gross *et al.*, 2009, 2013). Community ecologists are increasingly realizing that species' traits influence biotic interactions and ecosystem functions. With such increasing awareness, ecologists now quantify functional diversity using multivariate measures of trait variation within a community. A trait-based approach assessing community diversity might be as important as, and/or more meaningful than other community ecology approaches (e.g. species richness, or species composition) (McGill *et al.*, 2006; Cadotte *et al.*, 2011). A trait is any measurable physical, biochemical, behavioural, temporal or phenological characteristic of an individual organism that potentially affects its performance or fitness (Petchey & Gaston, 2006; Violle *et al.*, 2007; Cadotte *et al.*, 2011). Depending on their exact nature, traits are linked to species ecological strategies and directly influence community assemblage (Steneck & Dethier, 1994; Davies *et al.*, 2007). Traits influence species contribution to the ecosystem function as well through, for instance, differences in nutrient use and storage (Hillebrand & Matthiessen, 2009; Lavorel *et al.*, 2011; Lavorel, 2013).

Functional diversity was originally conceived as an alternative measure of (a) the ecological importance of species in a community (Walker, 1992; Chapin *et al.*, 1997), (b) how biodiversity affects specific ecosystem functions (Casanoves *et al.*, 2008), and (c) how species respond to environmental change (Grime, 1974; Westoby, 1998; Hooper *et al.*, 2002; Golodets *et al.*, 2009; Chalmandrier *et al.*, 2015). Most recently, knowledge of functional diversity and its incorporation into biodiversity conservation plans made authors question species assembly rules (Petchey & Gaston, 2002; Cornwell & Ackerly, 2009; Kraft *et al.*, 2009). Functional diversity measures can help capture information on biological function that is absent in measures of species diversity such as the extend of difference between species in term of their functional traits (Violle *et al.*, 2007). Patterns and changes in the range and distribution of functional trait values in a community can provide information on spatial and temporal variation in trait diversity, as well as on

processes that drive species assemblages and whether such assemblages are likely to contain redundant species (Tilman, 2001).

Recent trait-based studies in community ecology focus on analyses of trait dispersion among species to identify and estimate the relative importance of habitat filtering and niche differentiation (Luo *et al.*, 2016). Habitat filtering results in a relatively small range of trait values occurring in specific environmental conditions i.e., species co-existing in communities under habitat filtering usually exhibit similarity in life history, morphology and physiology (Grime, 2006). Alternatively, competition and the resulting limiting similarity may lead to communities containing dissimilar species, i.e. co-existing species under high competition intensity within a plant community may be expected to show differences in their biology. Therefore, the co-existence of species in a any given community likely results from the combined effect of habitat filtering and niche differentiation (Kraft *et al.*, 2009; Jung *et al.*, 2010). If habitat filtering occurs, then traits within communities are forced to converge leading to lower functional diversity than expected at random, whereas communities assembled under competition should show higher functional diversity than expected at random (Bernard-Verdier *et al.*, 2012; Maire *et al.*, 2012; Gross *et al.*, 2013).

Elevational gradients (as major environmental gradients) provide model systems for the study of factors that generate and structure biodiversity. A mid-elevation peak is an often-found pattern of taxonomic diversity along elevational profiles, mostly in relation with covarying resource and habitat availability. Functional diversity may vary in a coordinated manner with species diversity. The question is whether more functionally similar species can be packed into a confined functional space, or whether there may be a greater range of functions involved, in rich tropical plant communities? (Swenson, 2011). Moreover, with an increase in environmental adversity toward the upper limits of an elevational profile, strong habitat filtering, leading to trait convergence and decreasing functional diversity, is expected (Cornwell *et al.*, 2006; Grime, 2006; Baldeck *et al.*, 2013).

Epiphytic liverworts are ubiquitous components of bryophyte communities in tropical rainforests and provide a classic example of a taxonomically rich group with varied ecology and life-history (Gradstein & Pócs, 1989). They most often colonize tree trunks and branches without drawing water or food from living tissues of their hosts. The overwhelming abundance of epiphytic liverworts in cloud forests is considered an important factor in mitigating the negative effects of heavy rains, by increasing slope

stability and prevention of soil erosion. For such an understudied group, assessing the variation of informative functional traits among species and across elevation ranges is key to understanding the direction and magnitude of change in the long term (Murray *et al.*, 2002; Cornelissen *et al.*, 2007).

The aim of this study is to use a trait-based approach to assess the relationship between bryophyte species functional diversity and community assembly. Specifically, it addresses the following questions: (1) How do taxic and functional diversity components vary along the elevational gradient? (2) How do traits measured at species and community level respond to environmental changes along the gradient? (3) How do bryophyte species interact functionally with their abiotic and biotic environments? and (4) How do habitat filtering and niche differentiation influence bryophyte assemblages along this elevational gradient?

6.2. Materials and Methods

6.2.1. Study site and data collection

The study was carried out in Marojejy National Park, North-eastern Madagascar. Bryophytes were collected along an elevational transect at 200 m intervals from 250 m to 2050 m as described in Chapter 4. A description of the study area and details of data collection are provided in Chapter 4.

6.2.2. Trait selection and values

To date, the ecological and physiological functions of bryological traits have been poorly investigated (Ah-Peng *et al.*, 2014). I compiled data on morphological traits that (a) are likely to be related to resource use, life history, species defence, resistance to desiccation and photosynthetic activity, and (b) could be obtained for at least 95% of the taxa. Trait values for each taxon were collected from available literature and by direct measurements on curated plant specimens (Table A 4). The traits scored, typically as present/absent, are as follows:

Ocelli: unusually large leaf cells that often contain one or more larger-than-usual oil-bodies and lack chloroplasts.

Oil bodies: unique to liverworts, these are true membrane-bound organelles that contain terpenoid oils suspended in a carbohydrate and/or protein-rich matrix. Ninety percent of liverworts develop them. They are thought to deter herbivores or provide protection from cold and/or UV radiation (He *et al.*, 2013).

Lobules: smaller lobes of a complicate-bilobed leaf or a sac formed by an enrolled rear leaf margin (Malcolm & Malcolm, 2000). Lobules have long been interpreted as water-sacs allowing the plant to remain physiologically active when the colonies are subjected to persistent desiccating conditions.

Leaf surface papillae: developed in some liverwort species, they are thought to increase and maintain water uptake. By creating capillary channels on the leaf surface they appear to aid in retaining water and protecting regions of active cell division from dehydration (Proctor, 2008).

Trigones: wall thickenings in where three adjacent cells meet. The presence of trigones seems to be a xerophytic adaption in liverworts (Watson, 1914),

Underleaves: pseudoleaves on ventral stem surfaces. Their presence against the stem could favour the storage of intercepted water through capillarity in order to keep the plant moist and photosynthetically active (Ah-Peng *et al.*, 2017).

Size related traits: *gametophyte length*, *gametophyte width*, *stem diameter*, *leaf length*, *leaf width* and *elongation index* (gametophyte length/width ration). Those traits are related to growth and nutrient retention (Proctor & Tuba, 2002).

6.2.3. Data analyses

6.2.3.1. Quantifying functional diversity

Two multidimensional indices were used to characterize functional diversity following the framework proposed by Botta-Dukát (2005), Mason *et al.* (2005), Villéger *et al.* (2008) and Laliberté *et al.* (2010): functional evenness (*FEve*) and functional dispersion (*FDis*). Functional evenness is the degree to which the biomass of a community is distributed in niche space to allow effective utilisation of the entire range of resources available to it (Mason *et al.*, 2005). *FEve* describes the evenness of species abundance distributions in the functional trait space (Mason *et al.*, 2005; Villéger *et al.*, 2008). Functional dispersion was used to measure the weighted mean distance of individual species to their weighted centroid, where weights are their relative abundances. *FDis* describes the functional similarity of species in community in the trait space. Its variation indicates the species functional redundancy within a given scale and is measured from multiple traits (Laliberté *et al.*, 2010).

Functional evenness (*FEve*) is calculated as (Villéger *et al.*, 2008).

$$FEve = \frac{\sum_{e \in E} \min \left[\frac{dist(e)/(\frac{A_e}{A})}{\sum_{e' \in E} dist(e')/(\frac{A_{e'}}{A})}, \frac{1}{|S_c| - 1} \right] - \frac{1}{|S_c| - 1}}{1 - \frac{1}{|S_c| - 1}}$$

Functional dispersion (*FDis*) is calculated as (Laliberté *et al.*, 2010):

$$(1) c = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j} \quad (2) FDis = \frac{\sum a_j z_i}{\sum a_j}$$

Where c : weighted centroid in i -dimensional space, a_j : abundance of species j ; x_{ij} : attribute of species j for trait i ; z_j : distance of species j to the weighted centroid c .

We used linear regressions to evaluate whether bryophyte functional diversity indices increase with species richness.

6.2.3.2. Community weighted means (CWM) and Community weighted variances (CWV)

To determine the functional responses driving community assembly across the elevational gradient, we measured the community-weighted means (CWM) and variances (CWV) for each trait along the elevational transect. The CWM represents the mean of values present in the community weighted by the relative abundance of species bearing each value (Lavorel *et al.*, 2008).

Species weights in calculations were taken as the frequency of species occurrence, f , at each elevation. CWM_i is calculated as (Violle *et al.*, 2007; Bernard-Verdier *et al.*, 2012):

$$CWM_i = \sum_s f_{si} \times t_s$$

where f_{si} is the frequency of species s at elevation i and t_s is the vector of trait values for species s . Similarly, CWV_i is calculated as (Sonnier *et al.*, 2010; Bernard-Verdier *et al.*, 2012):

$$CWV_i = \sum_s f_{si} \times (t_s - CWM_i)^2$$

For binary traits CWM_i estimates the total frequency of species sharing the attribute, and CWV_i estimates the variance in this frequency.

6.2.3.3. Test for habitat filtering and niche differentiation

To assess the effect of habitat filtering and niche differentiation on community assembly, a null model approach was used to test whether the observed trait metrics

(CWM_i) differ from a random distribution. If habitat filtering is occurring then the range of trait values in observed communities should be below the null envelope (Cornwell & Ackerly, 2009).

I performed randomization of species abundances across elevations in order to break existing relationships between trait values and species abundance. Random assemblages were produced while constraining species richness per elevation. Weighted community traits were computed at each iteration and 2.5 and 97.5th centiles were then obtained from the null distribution to produce null confidence intervals across the elevation gradient.

Comparison of estimated CWM and CWV values with expectations from randomized data allows to detect significant deviations in observed patterns. Higher values of CWM compared to random simulations indicate higher trait values at community level, or higher frequency of species with a given attribute for binary traits, and symmetrically for values lower than expected. Such deviations are interpreted as evidence of ecological filtering towards high or low trait values (Bernard-Verdier *et al.*, 2012; Hulshof *et al.*, 2013). This can be thought of as analog to directional selection in evolution. Compared to random expectations, higher CWV values indicate significant variability in trait values, or for binary traits, high variability in frequency among species sharing similar attributes, symmetrically with lower CWV values. Such patterns are interpreted, in community-weighted traits, as patterns of ecological convergence/divergence for the considered traits and indirectly as evidence of competition or ecological filtering (Hulshof *et al.*, 2013; Kang *et al.*, 2017).

6.2.3.4. Relationships between environmental variables and functional diversities

For each functional diversity measure and CWM, I used a multiple general linear model to select the best multiple combinations of environmental variables that could predict community functional composition. AIC scores were compared for three models: linear, cubic, and quadratic polynomial, to determine the best fit. Models showing significant relationships at the 5% error level were retained. The model with the lowest AIC score and highest R² values was taken as best explaining the relationship between the observed CWM trait values and environmental variables. CWM for binary traits was logit-transformed prior to analysis. This allows us to consider models in the classical Gaussian framework for all response variables.

All analyses were conducted with the statistical software R (R Core Team, 2015) and the packages Ade4 (Dray, 2016), Permute (Simpson, 2016), Vegan (Oksanen *et al.*, 2015) and

FD (Laliberté *et al.*, 2010, 2015).

6.3. Results

6.3.1. Floristic and functional diversity of epiphytic liverworts along the elevational gradient

The epiphytic leafy liverwort flora of Marojejy National Park comprises 150 species, distributed in 44 genera and 18 families. The Lejeuneaceae were the most species-rich (73 species in 20 genera). As noted above (Chapter 4), species richness shows a hump-shaped pattern along the elevational gradient and peaks at mid-elevation (1250 m).

FEve shows an overall significant increase with altitude ($R^2 = 0.405$, $p < 0.05$). FDis increases significantly with elevation ($R^2 = 0.632$, $p < 0.01$) (Figure 32). No significant linear relationship is observed between species richness and the two measured functional diversity indexes (Figure 33).

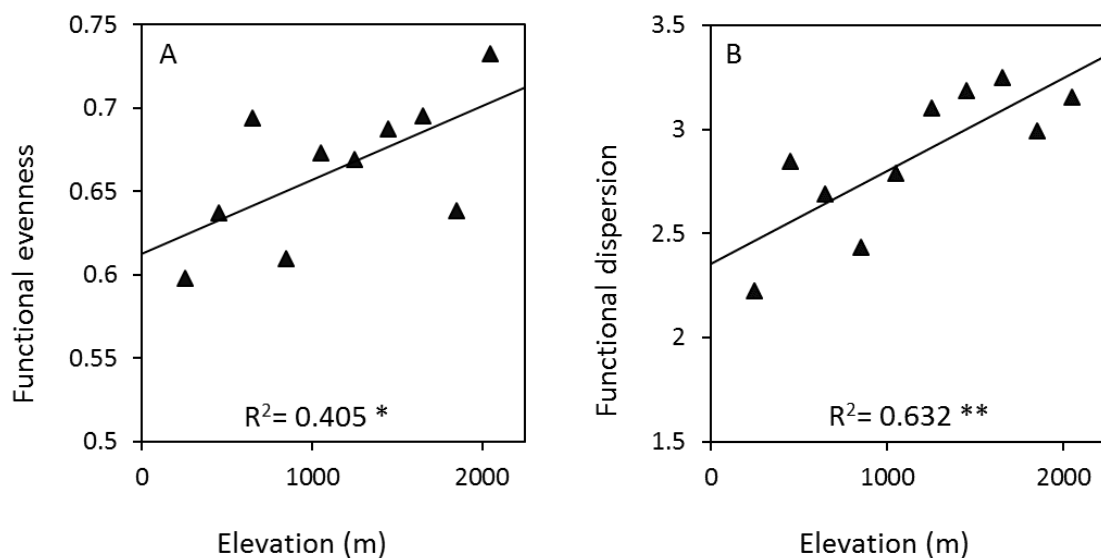


Figure 32: Pattern of Functional Diversity components with elevation. A: Functional evenness, B: Functional dispersion. R^2 value from a linear regression and 95% confidence level. (.) p -value < 0.1 * p -value < 0.05 , ** p -value < 0.01 , *** p -value < 0.001 .

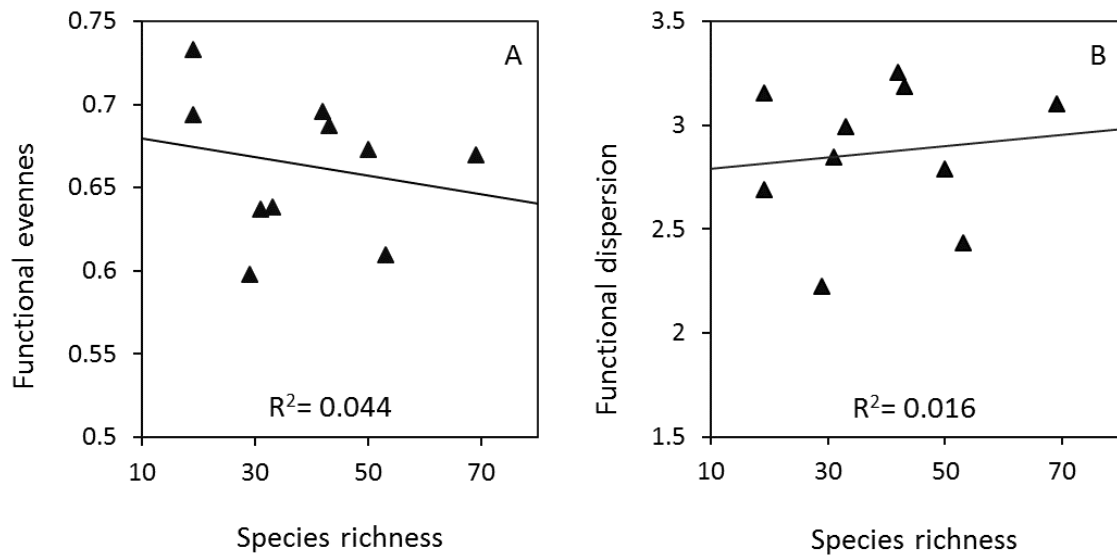


Figure 33: Linear regression between functional diversities and species richness. A: Functional evenness, B: Functional dispersion. R^2 value from a linear regression and 95% confidence level. (.) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

6.3.2. Variation in community trait means along the elevational gradient

Community weighted means (CWM) for size-related traits (i.e. leaf length, leaf width, gametophyte length, gametophyte width, and stem diameter) and for papillae and trigone presence significantly increased with increasing elevation. CWMs for lobule, ocelli and oil body presence significantly decrease with elevation. CWMs for underleaf presence did not show a significant relationship with elevation. A hump-shaped curve with elevation was found for elongation index (Figure 34, Table 11). Considering the intraspecific variability did not improve these relationships except for lobule presence and trigone presence, where the trigone presence decreases with increasing elevation and lobule presence increases with increasing elevation (Figure 36). The most dominant traits are leaf length ($R^2 = 0.9$, $p < 0.001$), gametophyte length ($R^2 = 0.92$, $p < 0.001$) and trigone presence ($R^2 = 0.87$, $p < 0.001$) (Table 12).

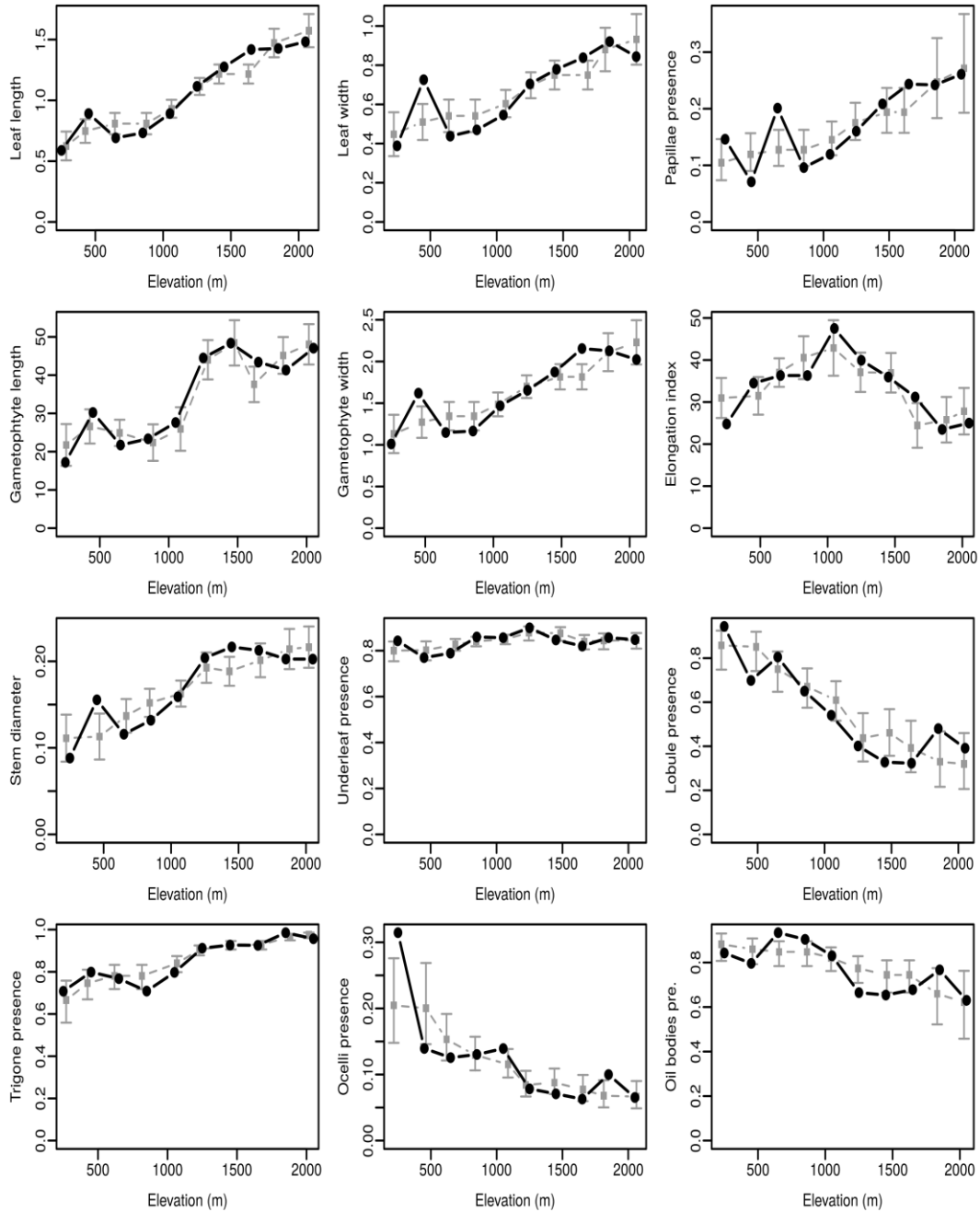


Figure 34: Distribution of community-weighted means (CWM) by elevation (circles) and values estimated by linear models from climatic variables (grey). Lines indicate the 95% confidence interval for modelled values.

Table 11: AIC for models of CWM with elevation. Only for papillae and trigone presence were cubic models retained. Multiple general linear model analysis was performed to select best multiple combinations of environmental variables that could predict community functional composition, selecting the model with the lowest Akaike Information Criteria (AIC). R² is shown for models with climate variables. AIClin (linear model), AICquad (quadric polynomial model), AICcub (cubic model).

Traits	AIClin	AICquad	AICcub	R ²	adjusted.R ²
Leaf length	-10.95	-9.54	-10.48	0.9	0.89
Leaf width	-11.24	-9.57	-8.57	0.73	0.7
Papillae presence	12.16	13.22	14.05	0.57	0.52
Gametophyte length	69.11	70.73	71.07	0.92	0.88
Gametophyte width	1.73	3.61	3.64	0.77	0.74
Elongation index	73.05	60.66	60.4	0.7	0.61
Stem diameter	-42.12	-42.5	-42.49	0.75	0.72
Underleaf presence	6.12	6.96	8.45	0.5	0.35
Lobule presence	23.48	16.24	18.24	0.74	0.7
Trigone presence	19.94	20.62	20.69	0.87	0.85
Ocelli presence	10.88	8.73	10.08	0.7	0.66
Oil body presence	20.49	22.26	20.41	0.5	0.44

Table 12: Regression coefficients for CWM models with elevation.

Traits	Est.	Std. Err.	T	p
Leaf length	0.000524	6.38E-05	8.2	***
Leaf width	0.000259	6.29E-05	4.12	**
Papillae presence	0.000631	0.000203	3.12	*
Gametophyte length	0.0166	0.00349	4.74	**
Gametophyte width	0.000607	0.00012	5.04	***
Elongation index	0.0445	0.0103	4.31	**
Stem diameter	6.49E-05	1.34E-05	4.83	**
Underleaf presence	0.000167	0.00015	1.11	ns
Lobule presence	-0.00511	0.00112	-4.57	**
Trigone presence	0.00158	0.000299	5.28	***
Ocelli presence	-0.00221	0.000769	-2.88	*
Oil body presence	-0.00081	0.000307	-2.64	*

(.) p-value < 0.1 * p-value < 0.05, ** p-value < 0.01, ***p-value < 0.001, ns not significant

6.3.3. Effect of environmental variables on community trait means along the elevational gradient

Leaf length, leaf width, gametophyte length, gametophyte width, papillae presence, and trigone presence exhibited significant correlations with canopy mean height (*cmea*). Conversely, oil body presence showed a significant positive correlation with *cmea*. Stem diameter and underleaf presence were negatively correlated with the mean temperature (temp.m^2), whilst lobule and ocelli presence exhibited significant positive correlation with this variable. Only the elongation index showed a significant correlation with the vapour pressure deficit (*vpd*) and weak correlation with relative humidity (*rh.m*) (Table 13). This indicates that a high percentage of variation in these traits is explained by the corresponding environmental variables.

Table 13: Regression coefficients for linear models of CWM with environmental variables.

Traits		Est.	Std.Err	T	p
Leaf length	<i>cmea</i>	-4.08E-02	0.00471	-8.65	***
Leaf width	<i>cmea</i>	-2.08E-02	0.00446	-4.67	**
Papillae presence	<i>cmea</i>	-4.99E-02	0.01532	-3.26	*
Gametophyte length	<i>cmea</i>	-1.73E+00	0.22753	-7.61	***
	<i>rh.m</i>	1.47E+01	6.07085	2.42	.
	$l(\text{vpd}^2)$	3.96E-03	0.00187	2.12	.
Gametophyte width	<i>cmea</i>	-4.73E-02	0.00916	-5.16	***
Elongation index	$l(\text{vpd}^2)$	-5.53E-03	0.00218	-2.54	*
	<i>rh.m</i>	-1.60E+01	7.04997	-2.26	.
Stem diameter	<i>temp.m</i>	-1.69E-02	0.00341	-4.96	**
Underleaf presence	$l(\text{temp.m}^2)$	-2.46E-03	0.00096	-2.57	*
	$l(\text{vpd}^2)$	-1.82E-05	1E-05	-1.81	ns
Lobule presence	$l(\text{temp.m}^2)$	1.07E-02	0.00227	4.72	**
Trigone presence	<i>cmea</i>	-1.29E-01	0.01803	-7.17	***
Ocelli presence	$l(\text{temp.m}^2)$	5.38E-03	0.00125	4.29	**
Oil body presence	<i>cmea</i>	6.51E-02	0.02307	2.82	***

cmea: mean canopy height, *vpd*: vapour pressure deficit, *temp.m*: mean temperature, *rh.m*: mean relative humidity. (.) p-value < 0.1 * p-value < 0.05, ** p-value < 0.01, ***p-value < 0.001, ns not significant

6.3.4. Habitat filtering along the elevational gradient

Trait filtering is indicated when trait means are lower than expected by chance. For each trait, deviations from the null model band were found at various elevations (Figure 35). We found evidence of trait filtering for lobule presence (1250-1650 m) and oil body presence (1250-1650 m), and at lower elevation for stem diameter (250-850 m) and gametophyte width (250 m, 560-850 m). Observed values of CWM were higher than expected at higher elevation for leaf length (1250-2050 m), leaf width (1650-1850m), gametophyte length (1250-2050 m), gametophyte width (1650-1850m), stem diameter (1250-1650m), papillae presence (1450-2050 m) and trigone presence (1250-2050 m). Only elongation index at mid elevation showed significant deviation above the null model. Underleaf and ocelli presence did not deviate from values predicted under the null model.

6.3.5. Trait divergence along the elevational gradient

Overall, communities displayed higher values of community weighted variance CWV than expected by chance at different elevations for leaf length (1650-1850 m), leaf width (450 m), papillae presence (1420-2050 m), elongation index (450-1250 m), gametophyte length (1250-1650 m and 2050 m), ocelli presence (250 m), and oil body presence (1250-1650 m), indicating that those traits have divergent distributions. This means that abundant species tend to have functional traits dissimilarity along the whole elevational gradient. Random dispersion of abundances is seen among local liverwort species for gametophyte width and stem diameter. Trait convergence is detected at 850-1250 m for underleaf presence, 1250-2050 m for trigone presence and 250-850 m for lobule presence (Figure 36).

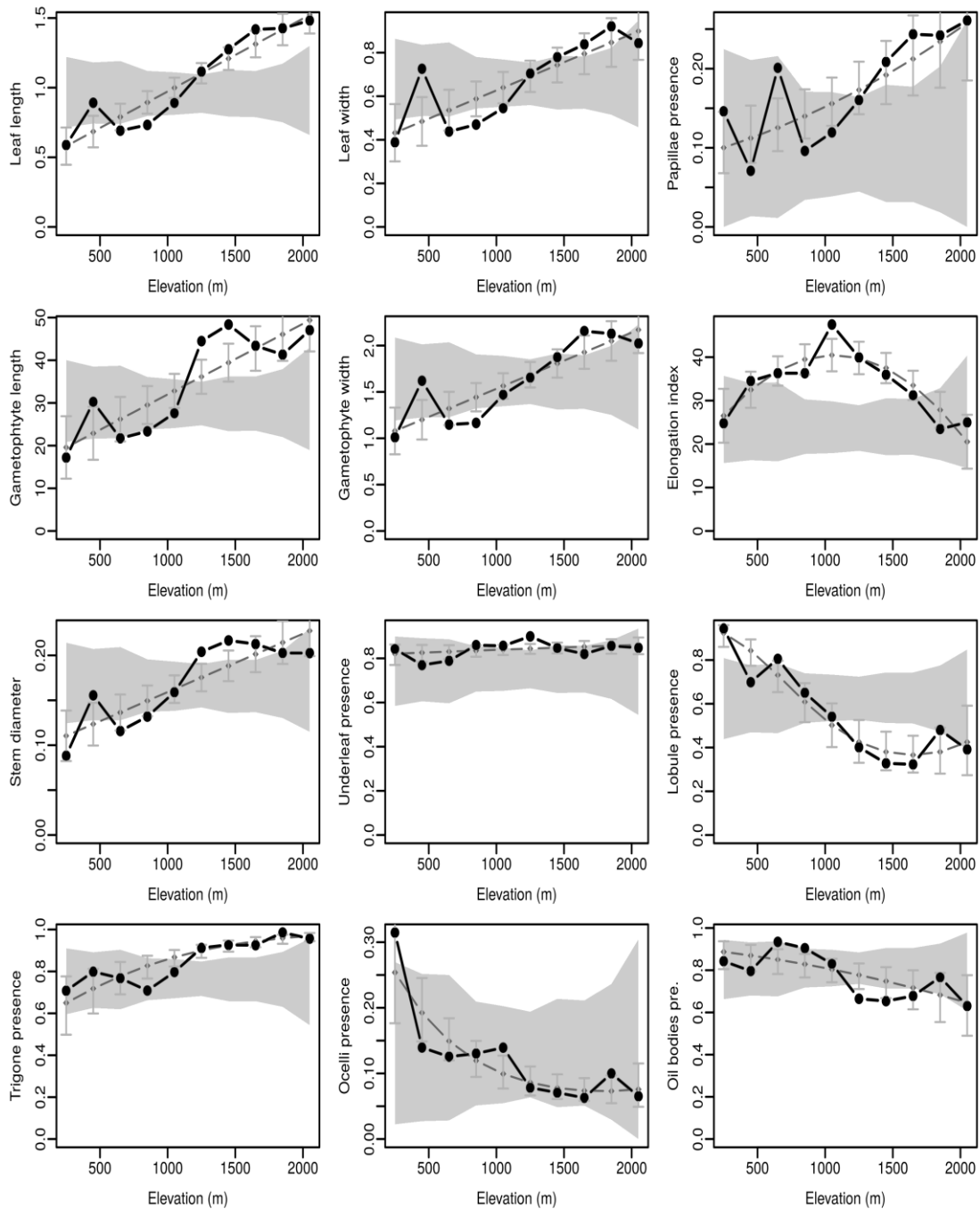


Figure 35: Distribution of community-weighted means (CWM) of traits along the elevational gradient. Envelope (grey) shows the 95% confidence interval under the null model of random community assembly. Squares indicates values estimated by linear models against elevation with 95% confidence interval.

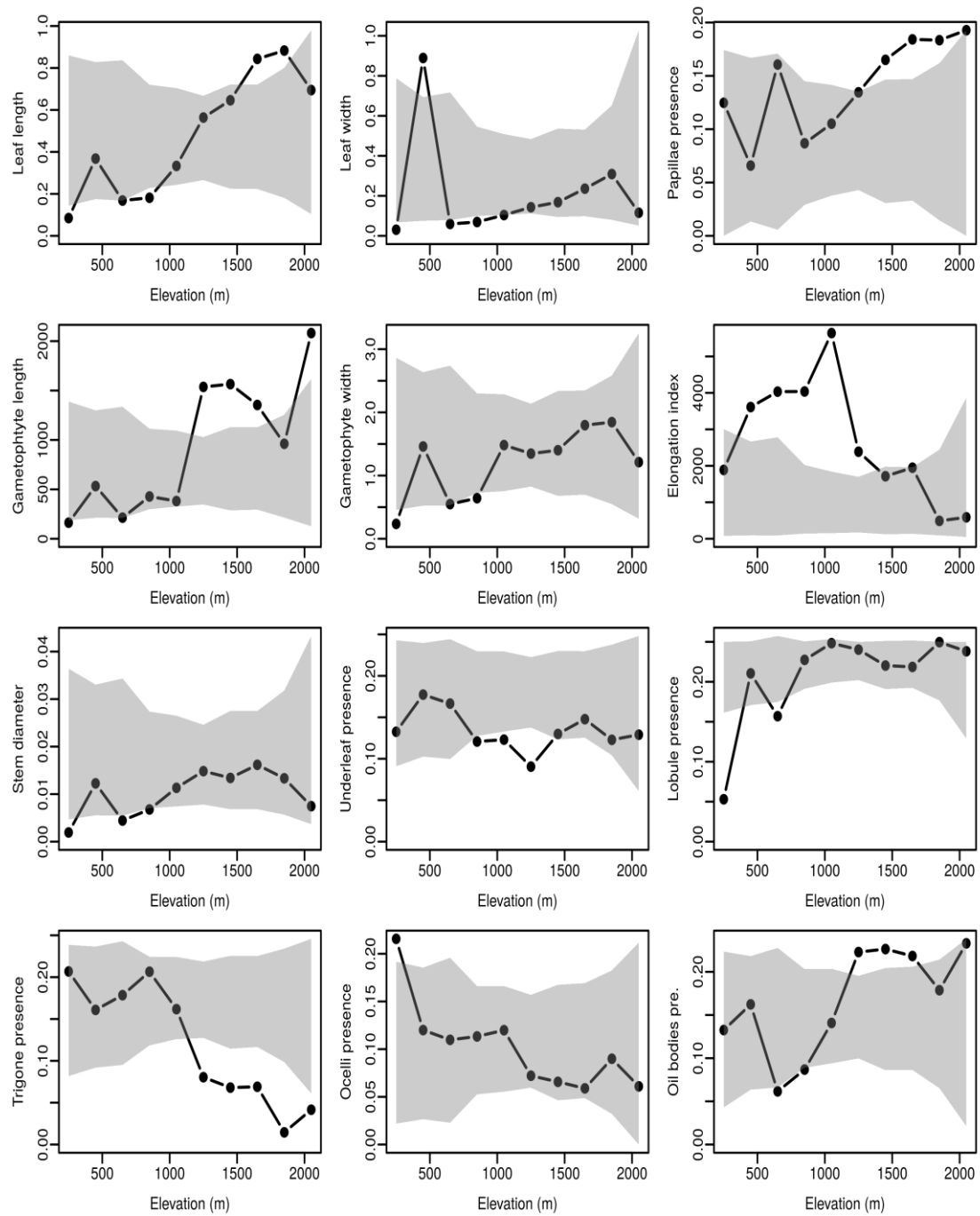


Figure 36: Distribution of community-weighted variances (CWV) of traits along the elevational gradient. The envelope (grey) shows the 95% confidence interval under the null model of random community assembly.

6.4. Discussion

Neither Community-Weighted Means (CWM) of trait values nor functional trait diversity metrics, have often been incorporated in combined analyses in ecosystems services assessments. But, to better understand species interaction and community assembly, they have recently been incorporated in biodiversity experiments (Mouillot *et al.*, 2011; Roscher *et al.*, 2012).

The trait-based analyses show that (1) functional evenness and functional dispersion increases significantly with elevation, (2) the pattern of distribution and variance of traits within communities along the elevational gradient are dependent on the nature of the considered traits (3) canopy height and temperature are the most powerful environmental variables shaping the pattern of CWM distribution, and (4) habitat filtering and niche differentiation both explained observed species abundance in communities, whilst habitat filtering is associated with trait convergence and is strongest at lower elevations. Niche differentiation associated with trait divergence occurs at higher elevation and is higher at the most species-rich sites.

6.4.1. Functional evenness, functional dispersion and floristic composition

Much attention has been focused on the use of functional traits, and their abundance and distribution in communities, in the exploration of relationships between biodiversity and ecosystem functioning (e.g. Halpern & Floeter, 2008; Cadotte *et al.*, 2009; Mouillot *et al.*, 2011; Roscher *et al.*, 2012). The positive relationship between functional evenness and elevation found here suggests a more regular functional distance among species as elevation increases (Villéger *et al.*, 2008). The fact that more individuals of the common species are recorded as elevation increases suggests liverwort functional traits are not evenly distributed along the elevational gradient. Functional dispersion quantifies the extent of functional similarity among species in the trait space. The increase in functional dispersion with elevation indicates low redundancy in the liverwort community. This highlights that new species added at each elevation are less similar than the existing species and reflects dissimilar functional traits in abundant species (Karadimou *et al.*, 2015, 2016).

6.4.2. Trait variation at different ecological scales

A main goal in this work was to determine which environmental factor(s) influence the variation and distribution of CWMs of liverworts traits across the elevational gradient. This study suggests that canopy height and temperature are the most powerful

environmental variables shaping the pattern of trait distributions. Relative humidity and vapour pressure deficit, on the other hand, have a weaker effect on trait variation and distribution among communities.

The leafy liverwort communities showed a clear functional response along the elevational gradient, as demonstrated by the observed clear pattern in community-weighted means for nine of the twelve traits (Figure 34). On one hand, the abundance-distribution of all traits related to plant size significantly increased with elevation, indicating that at high elevation there is more variation in plant size (Henriques *et al.*, 2017). Papillae and trigone presence are considered to be related to water retention and xerophytic adaptation respectively. Papillae facilitate water uptake by providing capillary space (Proctor, 1979), where elongated cells with trigones enhance water uptake from the surrounding environment. This study shows that the abundance of species with those traits also increases significantly with elevation, potentially as a response to the rougher environmental conditions at higher elevation. Lobules are often referred to as water sacs and, like papillae and trigones, an increasing CWM for lobule presence would have been expected. However, its CWMs were negatively related to increasing elevation. Since the presence of lobules is often found as characteristics of species of the Lejeuneaceae family, this pattern can be related to the fact that the Lejeuneaceae are most abundant at lower and mid-elevation. A similar result was found for ocelli presence. Although the functional role of ocelli is yet to be elucidated.

6.4.3. Habitat filtering and niche differentiation

Both habitat filtering and niche differentiation appear to be involved in structuring species abundances in the communities studied here. Our results add to the growing body of evidence of the joint effect of these two processes on community structure (Cornwell & Ackerly, 2009; Jung *et al.*, 2010; Mason *et al.*, 2011; Maire *et al.*, 2012). Figure 37 summarises these effects on a trait-by-trait basis for the whole gradient.

In the system studied here, trait filtering may occur toward both ends of the elevational gradient. This is in line with Mayfield & Levine (2010) hypothesis on the occurrence of ecological filtering at the extremities of an environmental gradient. According to Bernard-Verdier *et al.* (2012), this is due to the differential filtering of different traits along a gradient. The detection of ecological filtering is critically dependent of the studied trait. Different traits, related to different functional roles, were filtered at part along the elevational gradient. At low elevation, where diversity is lower, the range of

traits directly linked to growth and nutrient acquisition (gametophyte and leaf size) is reduced. Therefore, those traits were filtered out (Herben & Goldberg, 2014). This can be related to competition for light, given the fact that at low elevations in a tropical forest the canopy is continuous and the canopy height is the highest. This may account for the abundance of small and narrow species. At low elevations, for instance, the most abundant species include: *Bazzania nitida* (F.Weber) Grolle, *Ceratolejeunea stictophylla* Herzog ex Vanden Berghen, *Cololejeunea appressa* (A. Evans) Benedix, *Heteroscyphus dubius* (Gottsche) Schiffn., *Lejeunea confusa* E.W.Jones, and *Prionolejeunea grata* (Gottsche) Schiffn..

None of the studied traits, except for lobule and oil body presence, were specifically filtered at mid-elevation, suggesting that these provide the most favourable habitats for epiphytic liverworts. Interestingly, at mid-elevation trait variation is either randomly distributed or divergent (elongation index only) due perhaps to the relaxation of environmental constraints allowing for the coexistence of a wide range of functional strategies and therefore a peak of diversity at the centre of a gradient. Trait range reduction detected at mid-elevation suggests that trait filtering may also occur in more suitable habitats (Bernard-Verdier *et al.*, 2012).

Towards higher elevations, leaf length, leaf width and gametophyte length tend to be divergent in communities. This suggests that traits related to plant size coexist successfully, and species are less similar to each other (Funk *et al.*, 2008). This trend can be explained by the wide range in size exhibited by the most abundant species. Tall liverwort species such as *Herbertus dicranus* (Taylor ex Gottsche et al.) Trevis and *Mastigophora diclados* (Brid. ex F.Weber) Nees are about as abundant as small species such as *Conoscyphus trapezioides* (Sande Lac.) Schiffn. and *Drepanolejeunea physaefolia* (Gottsche) Steph. at higher elevations.

The divergence in leaf length, leaf width, gametophyte length, papillae presence, elongation index and oil body presence provide strong evidence of niche differentiation, although mechanisms such as limiting similarity or facilitation cannot be inferred here.

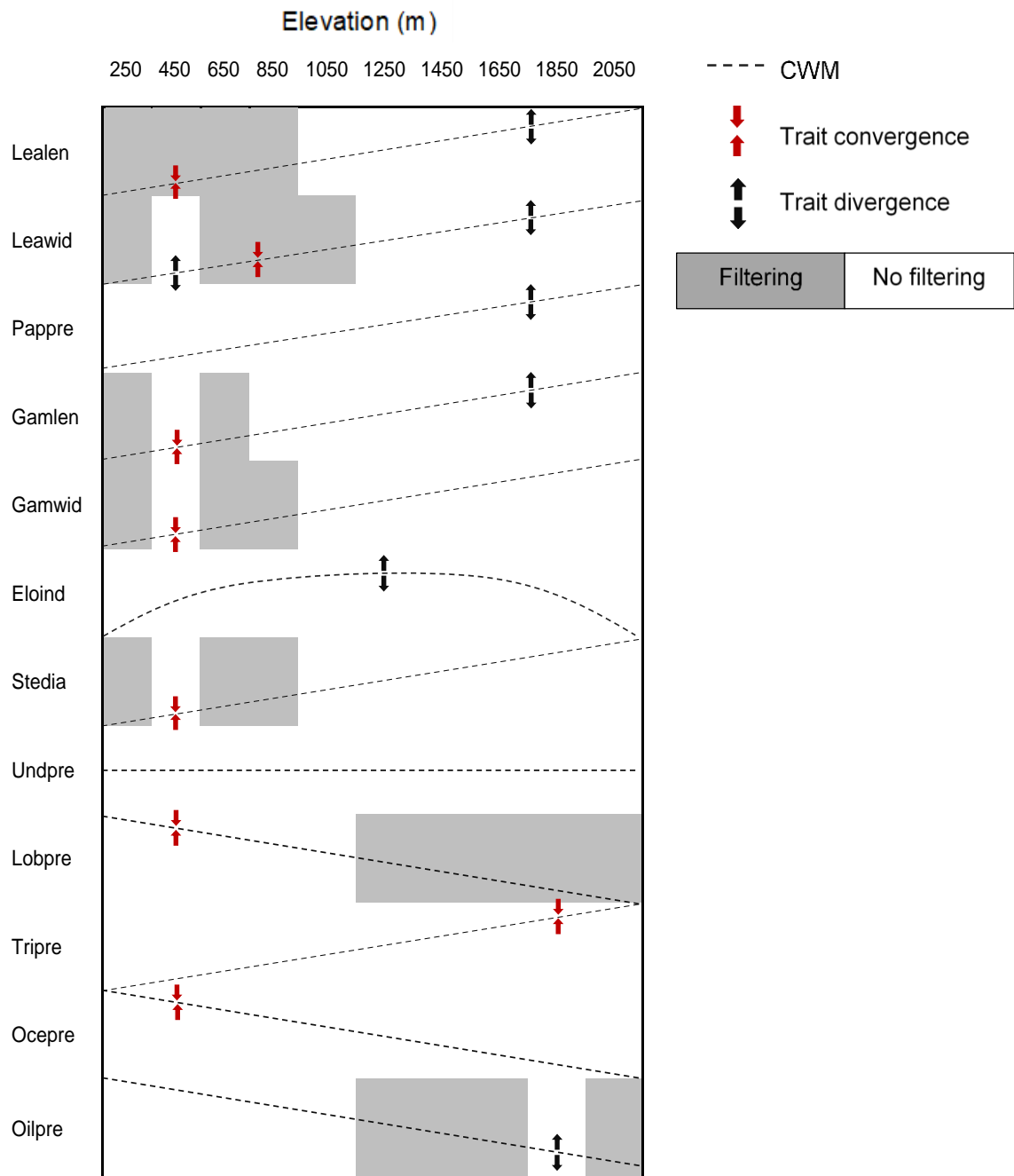


Figure 37: Schematic summary of the trends in functional community structure observed for eight functional traits along the elevational gradient. Adapted from Bernard-Verdier et al. (2012). Lealen: leaf length, Leawid: leaf width, Gamlen: gametophyte length, Gamwid: gametophyte width, Eloind: elongation index, Stedia: stem diameter, Pappre: papillae presence, Undpre: underleaf presence, Lobpre: lobule presence, Tripre: trigone presence, Ocepre: ocelli presence, Oilpre: oil body presence

6.4.4. Conclusions

This study provides evidence that assemblage of epiphytic liverwort community is driven by climatic conditions and vegetation structure, affecting the occurrence of species among and within communities. I demonstrate that traits tend to shift from convergent to divergent with an increasing elevation. Higher temperature and taller vegetation appear to have driven a strong functional convergence of size related traits (except for leaf width) at lower elevations but have allowed for divergence in these at higher elevation.

This is the first study to investigate bryophyte functional traits variation along an elevational gradient in Madagascar. Only morphological traits potentially related to resource use, life history, species defence, resistance to desiccation and photosynthetic activity were studied. However, other physiological traits related to features such as, photosynthetic capacity and carbon fixation need to be considered for further study and for a better understanding of the relationship between species composition and ecosystem processes.

CHAPTER 7
General Discussion

7. General Discussion

Bryophytes are among the least documented components of the rich Madagascan biodiversity. Information is lacking regarding their diversity, distribution and conservation effort in Madagascar. In this thesis, I have attempted to provide a floristic and biogeographical context for the bryophyte flora of Madagascar as well as to explore mechanisms structuring diversity and community structure in a model system - an elevational gradient on Marojejy massif in NE Madagascar. The main questions addressed in this thesis were: (1) what is the current state of knowledge of bryophytes of Madagascar? (2) what are the factors affecting the diversity and distribution patterns of epiphytic bryophytes along an elevational gradient? (3) how is biodiversity organised along the elevational gradient? (4) how do bryophyte species functionally interact with their abiotic and biotic environments through space and time? The conceptual framework of this thesis is detailed in [Figure 38](#).

Firstly, from available literature and herbarium data, I produced a general overview of the bryophytes of Madagascar by looking at the history of bryological exploration (Chapter 2) and providing a floristic and phytogeographic synthesis (Chapter 3). A chief objective of the bibliographical review was to summarise the state of bryophyte taxonomy for the island, allowing us to determine lacunae in knowledge and provide an assessment of priorities for future research.

I then undertook an analysis of diversity and structure of epiphytic bryophyte communities along an elevational gradient. Exploring the biodiversity-pattern and relationships in tropical mountain rainforest communities and effects of species richness on epiphytic community assemblages (Chapters 4), provided a better understanding of how bryophyte communities are structured along an elevational gradient and the main factors driving diversity and distribution patterns. Decomposing beta-diversity, with the additive partitioning of biodiversity and partitioning of beta diversity into species turnover and nestedness (Chapter 5), provided insights on the spatial variation in species composition of different communities, therefore a better understanding of the organisation of diversity. Measuring the different facets of functional diversity and community weighted mean trait variation along the elevational gradient (Chapter 6) elucidated the pattern of distribution and variance of traits within communities along the elevational gradient and identified the most powerful environmental variables shaping those patterns.

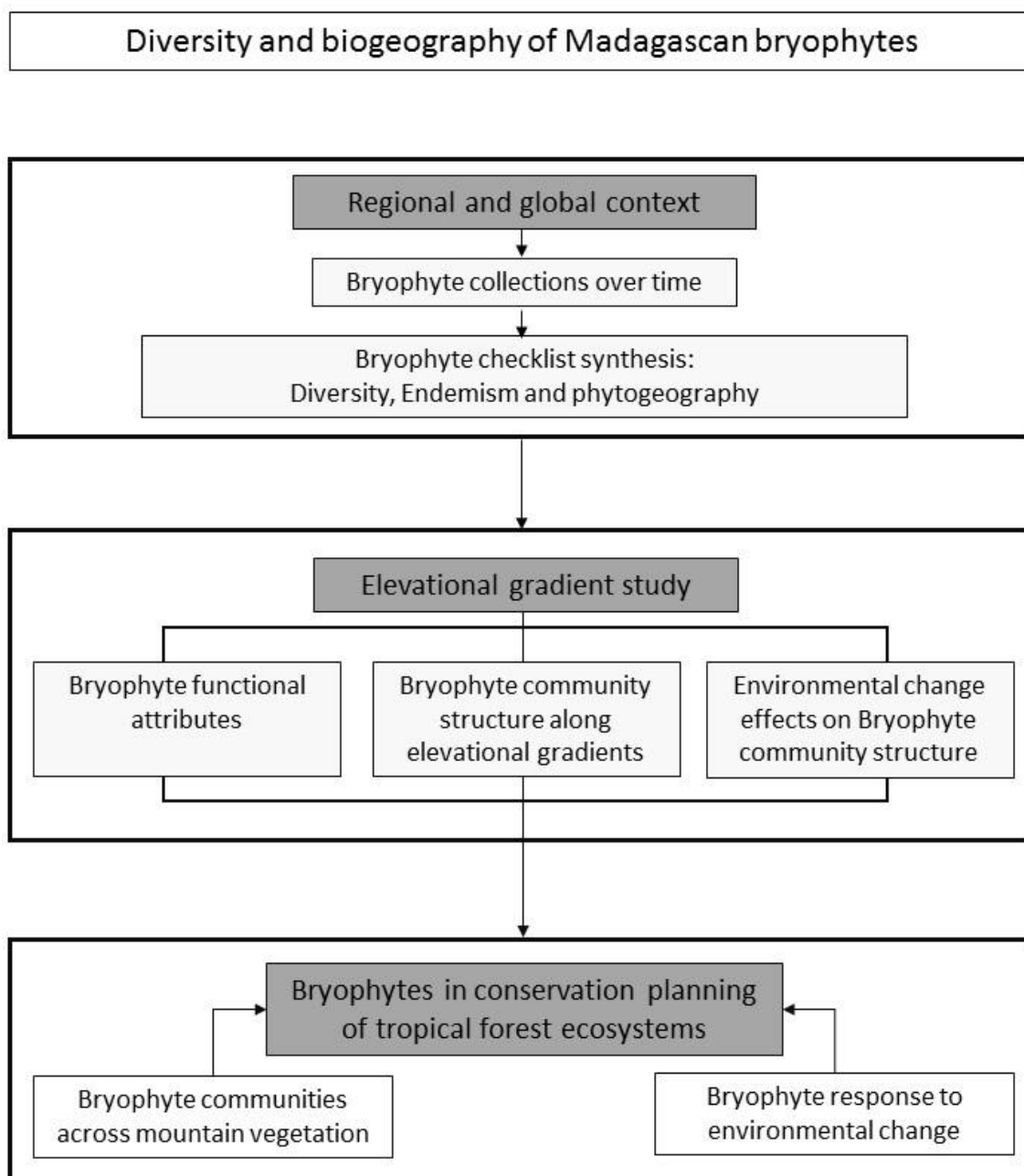


Figure 38: Conceptual framework of the thesis

7.1. The bryoflora of Madagascar

Floristic and ecological surveys, examination of historic specimens, and reviews of available literature have greatly increased our knowledge of the bryoflora of Madagascar. The floristic synthesis shows that bryophytes are important component of the biodiversity of Madagascar. Since the publication of the first checklist of Madagascan bryophytes

(Marline *et al.*, 2012), many additions have been identified from further bibliographical review and additional species determination. The bryophyte flora of Madagascar, originally enumerated at 1144 species and infraspecific, is now composed of 1188 species and infraspecific taxa. Species richness is dominated by mosses (760 mosses vs 425 liverworts), reflecting the global difference in diversity between the two groups. Only 3 hornworts are reported for Madagascar and this is the least documented of all three groups. Floristic studies must be based on a firm foundation of careful taxonomic studies. Identifying the phytogeography of bryophytes species is a time-consuming task to undertake given the lack of literature and study on species distributional range across the continents. However, during this study, I manage to gather information on plausible phytogeographical nature of 98% of the species recorded for the region. It was interesting to consider the possible origins and affinity of the Madagascar bryoflora. Excluding the species that may have been recently transported from Madagascar to its neighbouring Islands and vice-versa (40 % of the flora) the results show a high African affinity of the bryoflora confirming its position within the African bryoflora kingdom (Pócs & Geissler, 2002).

7.2. Community assembly and epiphytic bryophyte distribution

7.2.1. Diversity and distribution pattern

Epiphytic bryophyte communities are important components of tropical montane forests. They play important role in their nutrient cycling and water balance (Coxson, 1991; Curtis *et al.*, 2005; Ah-Peng *et al.*, 2017). In Marojejy National Park, epiphytic bryophytes show high diversity with 254 species, distributed over 39 families and 85 genera recorded. This number is likely to increase, given that many specimens could not be identified to species level due to poor taxonomic knowledge and in some cases to lack of fertile material from the ecological samples. Twenty-three species, representing 8.92% of those recorded for the study site, are endemic to Madagascar. This recorded diversity is comparable to ferns, for instance, where 274 species were recorded on the same gradient. If compared to the north-eastern slopes of the Manongarivo massif, for instance (50 to 1897 m asl), where a total of 176 species (including mosses and liverworts) and 100 unidentified species were recorded (Pócs & Geissler, 2002), this astounding diversity of the epiphytic bryophyte communities highlights the exceptional status of this mountain rainforest. The study complements the previous work of Goodman (2000a) on an

elevational inventory of the flora and fauna of the Park (reptiles, mammals, birds, ferns and vascular plants).

Among elevational gradient studies the most common pattern observed in tropical ecosystems is hump-shaped with a mid-elevational peak in richness. This pattern is observed for the epiphytic bryophytes of Marojejy National Park, north-eastern Madagascar, Piton de Neiges, La Réunion (3069 m), a much smaller island neighbouring Madagascar, continental Colombia (Ah-Peng *et al.*, 2012), and the Caribbean (Van Reenen & Gradstein, 1983) as well as for subtropical islands including the Azores and Canaries (Gabriel, Bardat, *et al.*, 2014). Species richness on tropical islands is much higher than in subtropical islands. In tropical ecosystems, small-ranged species contribute remarkably to the high species diversity and especially to the mid-elevational peak (Ah-Peng *et al.*, 2012; Henriques *et al.*, 2016). In this study, a large proportion (87%) of the recorded bryophytes have a range distribution covering half or less the length of the whole gradient. Those species occurred at different parts of the gradient. Marojejy forest's hard-elevational boundaries and environmental gradients may act as dispersal barriers and limit available habitat for a species and therefore restrict range sizes. This pattern is usually related to climatic variables, namely temperature, vapour pressure deficit and relative humidity. If the variation in elevational range sizes can be explained by shifts in niche range, rather than by differences in the length of these ranges, then elevationally narrow-ranged species are possibly more sensitive to environmental changes than larger-ranged species.

The mid-domain effect is one among many contributing factors that affecting spatial patterns of species richness (Colwell *et al.*, 2004, 2005). The Mid-domain effect is well demonstrated in Madagascar with a convincing example of a broad-scale gradient of species richness (Lees *et al.*, 1999; Colwell *et al.*, 2004; Pimm & Brown, 2004; Lees & Colwell, 2007). MDE has been discussed by several authors in the context of species distribution along a latitudinal gradient in Madagascar (Lees *et al.*, 1999; Kerr *et al.*, 2006; Currie & Kerr, 2007; Lees & Colwell, 2007). The Mid-Domain hypothesis predicts that small-ranged species are less affected by the MDE than large-ranged species; they are thus more likely to show the effects of underlying environmental drivers. Results of this study showed that the mid-domain null model, based on the idea of geometric constraints (Colwell & Lees, 2000), provides powerful explanation for the richness pattern along the Marojejy gradient.

7.2.2. Deconstruction of diversity components

Elevational gradient of species diversity is subject to the measurement of species diversity. If species occupy a similar ecological niche along the entire gradient, their distribution pattern is considered an outcome of interactions between species and the external environment factors.

7.2.2.1. Overall diversity

Ecological phenomena vary at multiple scales. Additive partitioning of diversity reveals the organisation of species diversity at hierarchically organised spatial scales and the underlying process(es) generating these patterns (Crist *et al.*, 2003; Gering *et al.*, 2003; Stendera & Johnson, 2005). It is crucial to know how much alpha (within-site diversity) and beta (among-site diversity) diversity contributes to the total diversity when interpreting the effect of different scales in community structure. To my knowledge, this is the first study to use additive partitioning to analyse the diversity pattern of bryophytes in Madagascar. In this scenario, the contribution of α and β diversity to total diversity were calculated from four hierarchical scales: microhabitat (50 cm²), quadrat (4 m²), plot (100 m²) and elevation (every 200 m). This approach showed that the variability of beta diversity is dependent on the spatial scale considered. Generally, more variation in species richness was found within the elevational scales, than within microplot scales, confirming that beta diversity at the largest sampling scale is the largest contributor to the total diversity (Gering *et al.*, 2003; Summerville & Crist, 2004; Rodriguez-Zaragoza *et al.*, 2011; Acosta-González *et al.*, 2013; Gabriel, Bardat, *et al.*, 2014). Furthermore, it indicates that bryophyte species among sample within each level are a subsample of the same species pool (Francisco-Ramos & Arias-González, 2013; Gao & Perry, 2016).

One of the most fundamental and recurrent challenges in beta diversity studies is to distinguish and quantify the pure “spatial turnover” component of beta diversity from that caused by variation in species richness between local communities or “nestedness” (Baselga, 2010). Very few studies have examined beta-diversity patterns of bryophytes or attempted to correlate those patterns with environmental predictors (Aranda *et al.*, 2014). Such studies contribute to a broader understanding of patterns in species turnover. Results from this study show evidence that the beta-diversity of epiphytic bryophyte assemblages is dominated by high spatial turnover due to recruitment of new species, a clear pattern for mountains (Baselga *et al.*, 2012). Such a pattern is often expected in areas with older assemblages due to speciation over time (Baselga *et al.*, 2012) and areas where

immigration rates decrease with increasing species numbers (Brown & Kodric-Brown, 1977). High species turnover due to species replacement has a significant consequence for conservation planning. If the overall beta-diversity is dominated by variation in species richness, areas capturing most of the species richness and significant ecological process can be prioritized for conservation planning. If, however, it is dominated by species replacement, all areas make a significant contribution to the local biodiversity and therefore should be considered important for conservation.

Another noteworthy finding (from cluster analysis) is that the low-elevation and the high-elevation plots shows distinct differences in species composition, with all the plots below 1000 m in one group and all plots above this in another, well-marked group. This marked and abrupt elevational differentiation in bryophyte communities is interesting, bearing in mind that these organisms can disperse over long and short distances. The observed differentiation may reflect climatic differences and habitat heterogeneity among sites.

7.2.2.2. Functional diversity

Biodiversity is usually measured with reference to the numbers of species or other indices based on the taxonomical composition of any given community. However, measurement of biodiversity should also include functional components of species (and by extension communities), which reflect their important structural properties (Moretti & Legg, 2009). By adopting a trait-based approach, I demonstrate that results from studies using species richness and composition, can differ markedly from those including species functional traits. However, the two approaches capture different aspects of biodiversity and provide complementary mechanism for better understanding processes underlying bryophyte assembly (Leingärtner *et al.*, 2014; Bastias *et al.*, 2017). The pattern of the distribution and variance of traits within communities along the elevational gradient are dependent on the nature of the considered traits and environmental conditions. This suggests that a general trend for such a pattern along an environmental gradient can not be expected.

Furthermore, this study suggests that habitat filtering and niche differentiation along the same transect both explained observed species abundance in communities. Whilst habitat filtering is associated with trait **convergence** and is strongest at lower elevations, niche differentiation associated with trait **divergence** occurs at higher elevations and is higher at the most species-rich sites. These results are in line with Harpole & Tilman,

(2007) study which found that the number of available niches for plants increases with environmental severity which lead to a higher level of species coexistence, and that plant response to environmental factors is usually driven by a combination of traits (Lavorel & Garnier, 2002; McGill *et al.*, 2006; Gross *et al.*, 2007).

7.2.3. Implication for conservation

It is now widely recognized that bryophyte conservation should be considered as an integrated part of an overall biodiversity conservation strategy, rather than being marginalized. Most ecological studies investigate relationships between species richness and diversity and ecological factors that might explain them (Vanderpoorten & Engels, 2003; Kubešová & Chytrý, 2005; Sun *et al.*, 2013). The extreme concentration of bryophyte diversity makes the conservation of bryophytes probably easier in comparison with other groups of organisms. Management plans invariably deal with fauna and vascular flora, with bryophytes rarely considered in conservation planning. There is simply insufficient information concerning their ecology and biology. This challenge needs to be taken up.

This study uses additive partitioning of species diversity to determine the spatial scale contributing most to total epiphytic bryophytes diversity and to identify the contribution of nestedness and species turnover to overall biodiversity along an elevational gradient in the North East of Madagascar. Such study is crucial for the better understanding of central biogeographic, ecological and conservation issues. For conservation purposes, the distinction is essential, because nestedness and spatial turnover patterns also require specific conservation strategies (Wright & Reeves, 1992). Species poor sites could, paradoxically, require devoted conservation efforts: in this study the poorest areas, mostly composed of rare species, are found at both limits of the elevational gradient. A step towards recommending a conservation plan should be to distinguish impoverished zones from replacement zones, to enable the prioritization of the richest sites.

7.3. Perspectives and future research

Much work needs to be done to complete our knowledge of the Madagascan bryophyte flora. The checklist of bryophytes produced during this study provides a comprehensive list of bryophytes known from Madagascar based on literature records and additional collections, as well as provide information on the type specimens for endemic species, which will promote future work on the Madagascan bryoflora. Since much of the

original bryological exploration of Madagascar took place during the late 1800's (Dorr, 1997), it is not known what proportion, of the recorded taxa have been lost due to anthropogenic destruction of habitats for farming and logging (Marline *et al.* 2012). Furthermore, large parts of the country remain totally unexplored for bryophytes, and only a small part of the island has received attention from bryologists (mainly areas nowadays defined as protected areas and primary forests and the rainforests). New inventories of intact and unexplored habitats on the island should prove invaluable for verifying many of the old records presented in this checklist and will undoubtedly reveal many new and interesting records for the island as well as previously undescribed species. Geo-referencing species occurrences according to the specimen information of the locality description, using geographic gazetteers and supporting cartography, could also be useful as preliminary work to aid further research e.g. taxonomic revision, species distribution modelling etc.

The approach of stacking individual species distribution models to generate maps of potential richness has become widely used in conservation planning and the design of reserve networks (Guisan & Rahbek, 2011), or the identification of suitable areas for threatened or otherwise rare species (Graham & Hijmans, 2006; Pearson *et al.*, 2006; Williams *et al.*, 2009). It is a useful tool to integrate poorly known and inconspicuous groups into the process of designing priority areas. Biogeographic patterns of endemism have been previously investigated for the Malagasy fauna including mammals (Martin, 2000), reptiles and amphibians (Raxworthy & Nussbaum, 1995, 1996; Lees *et al.*, 1999; Brown *et al.*, 2016). Such study is useful in identifying important areas for bryophytes in Madagascar. In particular, analyses relating to how well such areas are protected and whether or not the areas for bryophytes coincide with those for other taxa.

Quantifying phylogenetic diversity: A phylogenetic approach would contribute greatly to understanding the distribution of species functional traits with elevation, and to what extent this may be controlled by abiotic factors. Phylogenetic diversity quantifies the biodiversity value of localities and reflects “evolutionary history” (Faith & Baker, 2006). The phylogenetic diversity of assemblages is generally correlated with species richness. Predicting the relationship between PD and the elevational gradient, whether the PD increases or decreases with the elevation can be used to estimate the potential loss of PD or areas with high PD. It highlights the utility of PD assessments for setting priorities for biodiversity conservation. Determining whether some ecological traits are phylogenetically conserved would contribute to understand ecosystem functioning, offer

increased predictive power in assessing ecosystem dynamics in response to global change and allow us to evaluate whether evolutionary life history characters are correlated with elevation and patterns of species richness.

7.4. Concluding remarks

This combination of floristics and community ecology, is the first multifaceted diversity study on the bryophytes of Madagascar. This thesis provided interesting insights into bryophyte diversity, distribution patterns and functional ecology, and the factors responsible for structuring epiphytic bryophyte communities in tropical rainforest, using a taxonomic and functional approach. The results showed that species richness distribution has a unimodal response to elevation, peaking at mid-elevation. My results suggest that the mid-domain-effect is the most effective predictor of species richness, but environmental variables such as mean temperature, relative humidity, vapour deficit pressure and canopy height also play important roles in shaping the richness pattern. Throughout the gradient, species dissimilarity due to replacement (species turnover) contributes the most to variation in species composition between sites. Environmental filtering and niche differentiation jointly determine species occurrence and distribution within communities. Such information and understanding of the dominant functional traits in bryophyte assemblages could be useful in the evaluation of the condition of the tropical forest ecosystems as a basis for conservation planning. Forest communities show variation in composition of vascular plants of different growth/life forms (trees, shrubs, ferns, and other herbaceous plants) along gradients of site conditions (nutrient status and moisture conditions of the substrate) and of microclimate conditions of light, humidity and temperature from ground level up into the canopy. Such conditions may also vary along stand development stages from disturbance towards mature forest. The variation in the suite of bryophyte species and their functional traits along these site and micro-climate gradients across forest communities, may be useful indicators of forest condition change towards stand maturity. The response of bryophyte assemblages within changed floristic and structural composition of the forest after disturbance due to resource harvesting, cyclones and tree falls etc. may be indicative of the resilience of the forests to such disturbance events (Figure 38). Similarly, bryophyte response to climate change, in addition to natural and anthropogenic disturbances, may guide effective measures to ensure recovery of the biodiversity and ecological processes under such changed

conditions. The understanding of bryophyte functional attributes and their dynamics may become a crucial component in conservation planning and sustainable forest management.

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Appendix

Appendix 1: Checklist of the bryophytes of Madagascar (Marline *et al.*, 2012)

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Checklist of the bryophytes of Madagascar

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Abstract – This updated checklist of the bryophytes of Madagascar was compiled from the literature, herbarium and recent collections. A total of 1144 species and infraspecific taxa are recorded for Madagascar composed of 751 mosses, 390 liverworts and 3 hornworts. 28.67% of the species reported for the Island are endemics. Twenty-four taxa are newly recorded for Madagascar and two of them, *Fissidens cyathaeicola* Brugg.Nann. and *Taxithelium nepalense* (Schwägr.) Broth. are reported for the first time for the Sub-Saharan Africa region.

Hornworts / liverworts / mosses / Madagascar

INTRODUCTION

Madagascar is located in the Indian Ocean, between 11°57' and 25°39' latitude, 400 km from the eastern coast of Africa. It is the world's fourth largest island, with a total area of 590 000 km², the distance between Cap d'Ambre

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(North) and Cap Sainte Marie (South) is nearly 1570 km, and the distance from West to East is around 560 km (Ingram & Dawson, 2005). The island consists of a central plateau of volcanic origin which culminates to the north in peaks over 2800 meters. To the East, the plateau falls directly and abruptly onto a narrow coastal plain, while in the West it descends more slowly to a broader plain, along the Mozambique Channel.

The island is considered a biodiversity hot spot: 85% of the flora (Gautier & Goodman, 2003) and 90% of the fauna are endemics (Goodman, 2008). The tropical forests of Madagascar are among the highest priority areas in the world for biodiversity conservation (Myers *et al.*, 2000). Eighty percent of Madagascar's original forests have disappeared in the 1500-2000 years since the arrival of the first humans (Harper *et al.*, 2007). At present, only 12% of the surface of the island is covered by natural forest. These remnant forests are highly endangered by threat of deforestation. Cultivation involving slash and burn agriculture (locally called tavy) is the main cause of deforestation. Tavy consists of clearing and burning native forest. The burnt area is used for various plantations until the soils are impoverished, and then abandoned (Ingram & Dawson, 2005). The increasing population and the absence of resources and techniques to improve agricultural productivity and pasture lands threaten to destroy what remains of this unique biology (Sussman *et al.*, 1994).

The classification by Du Puy and Morat (1996) divides the primary vegetation of Madagascar into two formations: the evergreen and the deciduous formations.

The **evergreen formations** (East and Center) are: Coastal forest (East); Evergreen humid forest, low elevation (0-800 m); Evergreen humid forest, mid elevation (800-1800 m); Evergreen humid forest, lower montagne (1800-2000 m); Mountain, Schrubland (*Philippia*) (> 1800 m); Evergreen, sclerophyllous (*Uapaca*) woodland (800-2000 m) and Marshland (0-800 m)

The **deciduous formations** (West and South) are: Coastal forest (West); Deciduous, seasonally dry, western forest (0-800 m); Deciduous, dry, southern forest and schrubland (0-300 m).

The distribution of different vegetation formations in Madagascar is shown in Fig. 1.

The study on the flora of Madagascar has, for a long time, focused on vascular plants, with few studies being undertaken on bryophytes. Indeed, it was only during the 19th century that collectors first began to collect bryophytes in the Island (Dorr, 1997). There are more than 40 botanists that collected bryophytes on the island during the 19th century. The majority of which were French botanists and explorers. Collections through this period, by Cardot, Tixier, Cramers, Chénagon, and Perrier de la Bathie are mainly located at Paris herbarium (PC). Biographical data of bryophyte collectors are reported in Dorr (1997). The oldest collections are located at PC. From 1960, date of the independence of Madagascar, duplicates of the collections were hosted at the National Herbarium of Madagascar (TAN), of which more than a thousand samples still need to be identified. Nowadays, collections of Madagascan bryophytes are hosted in different herbaria around the world.

This article aims to provide a comprehensive list of bryophytes from Madagascar based on literature records and additional collections, as well as provide information on the type specimens for endemic species. We hope that this preliminary work will be helpful for other bryologists and will stimulate and facilitate future work on the bryoflora of Madagascar.

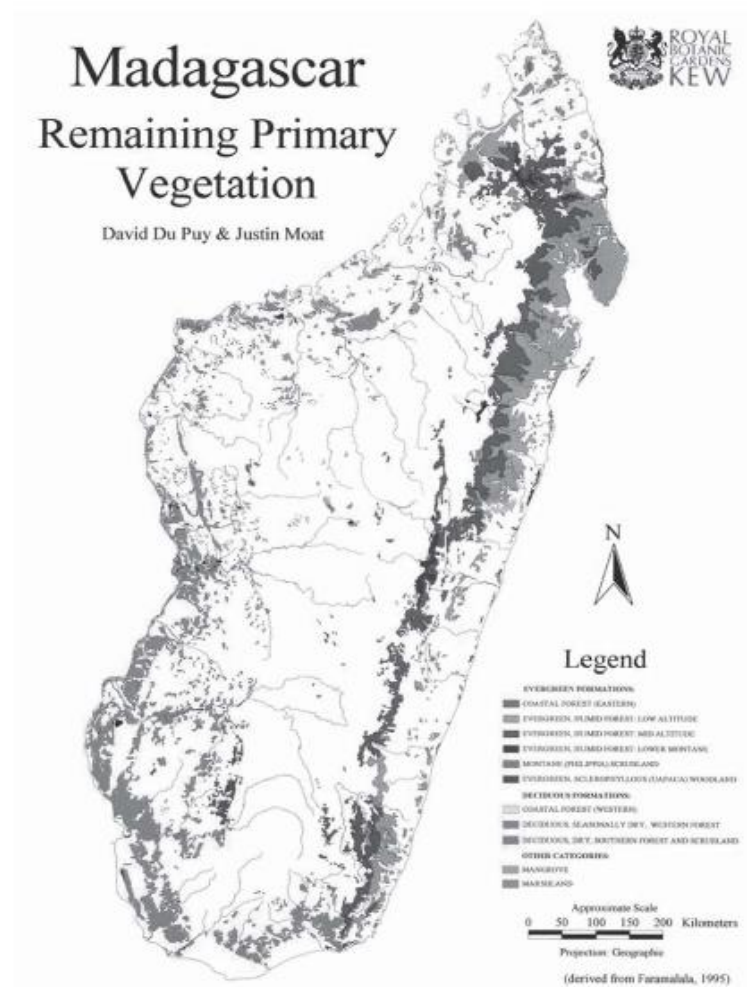


Fig. 1. Vegetation map of Madagascar (Du Puy & Morat, 1996) (reproduction with the permission of IRD).

METHODS

This checklist was compiled from the literature, data from various herbaria, and recent collections by the authors. This work was greatly facilitated by the ground work of O'Shea (2006) and Wigginton (2009) for their respective checklists of mosses, liverworts and hornworts for sub-Saharan Africa.

Presentation of the list

– Synopsis of families and genera

Families are ranked alphabetically within each order and sub order. The numbers in brackets against each genus indicate the number of taxa within the genus. Synopses of genera and family are based on the work of Crandall-Stotler *et al.* (2009) for liverworts, Renzaglia *et al.* (2009) for hornworts and Goffinet *et al.* (2009) for mosses.

– Format of the list

The taxa are arranged alphabetically within the three divisions of bryophytes: Marchantiophyta (liverworts), Anthocerotophyta (hornworts) and Bryophyta (mosses) and within each family. Scientific names appear in *bold italic* type followed by the authors who described the taxa. Endemic taxa are followed by “**End**”. New records from Madagascar are preceded by *. Herbarium abbreviations follow Thiers (2010). Uncompletely identified species that have been reported by O’Shea (2006) and Wigginton (2009) are taken into account in this checklist.

The references following each taxon are the record of the presence of the taxon in Madagascar, it refers mainly to the work of O’Shea (2006) and Wigginton (2009).

For new records from herbarium specimens, the references following the taxa are: locality, habitat, altitude, geographic coordinates, collection date, collector(s), collector’s number, and herbarium.

For new records that were recently collected during the BRYOLAT expedition in November 2009 and other fieldtrips, as well as for type specimen information, references following the species names are: locality, microhabitat, geographic coordinates, date, collector, collection number, and determinator.

When “unknown” is specified after type, this means that no information was given by the specimens, except “Madagascar” as main locality. “N.S.” is used when the holotype or herbarium are “not specified” and “#” is used when the information is considered doubtful.

RESULTS**Synopsis of the genera and families of Liverworts, Hornworts and Mosses****DIVISION MARCHANTIOPHYTA (LIVERWORTS)****CLASS MARCHANTIOPSIDA****Subclass Marchantiidae****ORDER MARCHANTIALES**Family **Aytoniaceae***Asterella* (2)*Plagiochasma* (1)Family **Cyathodiaceae***Cyathodium* (1)Family **Dumortieraceae***Dumortiera* (1)Family **Marchantiaceae***Marchantia* (2)Family **Ricciaceae***Riccia* (5)Family **Targioniaceae***Targionia* (2)

CLASS JUNGERMANNIOPSIDA

- Subclass Pelliidae**
ORDER FOSSOMBRONIALES
 Family **Fossombroniaceae**
Fossombronia (1)
ORDER PALLAVICINIALES
 Family **Pallaviciniaceae**
Pallavicinia (1)
Symphyogyna (2)
Symphyogynopsis (1)
Subclass Metzgeriidae
ORDER PLEUROZIALES
 Family **Pleuroziaceae**
Pleurozia (1)
ORDER METZGERIALES
 Family **Aneuraceae**
Aneura (1)
Riccardia (9)
 Family **Metzgeriaceae**
Metzgeria (6)
Subclass Jungermanniidae
ORDER PORELLALES
 Family **Frullaniaceae**
Frullania (38)
 Family **Lejeuneaceae**
Acanthocoleus (2)
Acrolejeunea (3)
Archilejeunea (4)
Brachiolejeunea (1)
Bryopteris (1)
Caudalejeunea (4)
Ceratolejeunea (6)
Cheilolejeunea (14)
Cololejeunea (54)
Colura (9)
Diplasiolejeunea (26)
Drepanolejeunea (9)
Frullanoides (1)
Haptolejeunea (1)
Lejeunea (22)
Lepidolejeunea (1)
Leptolejeunea (2)
Lopholejeunea (12)
Marchesinia (2)
Mastigolejeunea (2)
Metalejeunea (1)
Microlejeunea (5)
Odontolejeunea (1)
Otolejeunea (3)
Prionolejeunea (1)
Ptychanthus (1)
Pycnolejeunea (1)
- Schiffneriolejeunea* (6)
Symbiezidium (2)
Taxilejeunea (3)
Thysananthus (1)
Xylolejeunea (1)
 Family **Porellaceae**
Porella (5)
 Family **Radulaceae**
Radula (11)
ORDER JUNGERMANNIALES
 Family **Adelanthaceae**
Adelanthus (2)
 Family **Arnelliaceae**
Gongylanthus (1)
 Family **Balantiopsidaceae**
Isotachis (1)
 Family **Calypogeiaceae**
Calypogeia (7)
Mnioloma (1)
 Family **Cephaloziaceae**
Cephalozia (1)
Iwatsukia (1)
 Family **Cephaloziellaceae**
Amphicephalozia (1)
Cephaloziella (2)
Cylindrocolea (2)
Kymatocalyx (3)
 Family **Herbertaceae**
Herbertus (2)
 Family **Jamesoniellaceae**
Cryptochila (1)
Cuspidatula (1)
Denotarisia (1)
Syzygiella (3)
 Family **Jungermanniaceae**
Gottschelia (1)
Notoscyphus (1)
Solenostoma (4)
 Family **Lepidoziaceae**
Amazoopsis (1)
Bazzania (11)
Kurzia (2)
Lepidozia (2)
Telaranea (3)
 Family **Lophocoleaceae**
Chiloscyphus (8)
Clasmatocolea (1)
Conoscyphus (1)
Heteroscyphus (2)
Leptoscyphus (2)

Family **Mastigophoraceae***Mastigophora* (1)Family **Plagiochilaceae***Plagiochila* (21)Family **Scapaniaceae***Anastrophyllum* (1)*Andrewsianthus* (1)*Plicanthus* (2)Family **Schistochilaceae***Gottschea* (1)*Schistochila* (2)**DIVISION ANTHOCEROTOPHYTA (HORNWORTS)**

CLASS ANTHOCEROTOPSIDA

ORDER ANTHOCEROTALES

Family **Anthocerotaceae***Anthoceros* (1)*Dendroceros* (1)

ORDER NOTOTHYLADALES

Family **Notothyladaceae***Phaeoceros* (1)**DIVISION BRYOPHYTA (MOSS)****Superclass I**

CLASS SPHAGNOPSIDA

ORDER SPHAGNALES

Family **Sphagnaceae***Sphagnum* (16)**Superclass II**

CLASS ANDREAEOPSIDA

ORDER ANDREAEALES

Family **Andreaeaceae***Andreaea* (2)**Superclass III**

CLASS POLYTRICHOPSIDA

ORDER POLYTRICHALES

Family **Polytrichaceae***Atrichum* (1)*Pogonatum* (4)*Polytrichastrum* (1)*Polytrichum* (5)

CLASS BRYOPSIDA

SUBCLASS FUNARIIDAE

ORDER GIGASPERMALES

Family **Gigaspermaceae***Gigaspermum* (1)*Oedipodiella* (1)

ORDER FUNARIALES

Family **Funariaceae***Entosthodon* (4)*Funaria* (5)*Physcomitrium* (2)

SUBCLASS DICRANIDAE

ORDER GRIMMIALES

Family **Grimmiaceae***Grimmia* (3)*Bucklandiella* (1)Family **Ptychomitriaceae***Ptychomitrium* (2)

ORDER ARCHIDIALES

Family **Archidiaceae***Archidium* (2)

ORDER DICRANALES

Family **Bruchiaceae***Trematodon* (7)Family **Calymperaceae***Calymperes* (10)*Leucophanes* (3)*Mithyridium* (2)*Octoblepharum* (2)*Syrrhopodon* (23)Family **Ditrichaceae***Ceratodon* (1)*Distichium* (1)*Ditrichum* (4)*Garckea* (1)*Pleuridium* (1)Family **Dicranaceae***Anisothecium* (1)*Aongstroemia* (2)*Dicranella* (6)*Dicranoloma* (3)*Dicranum* (1)*Holomitrium* (11)*Leptotrichella* (2)*Leucoloma* (55)*Microcampylopus* (1)*Pseudephemerum* (1)Family **Erpodiaceae***Erpodium* (2)Family **Eustichiaceae***Eustichia* (1)

- Family **Fissidentaceae**
Fissidens (40)
 Family **Leucobryaceae**
Atractylocarpus (1)
Campylopus (23)
Leucobryum (19)
Ochrobryum (1)
 Family **Rhachitheciaceae**
Rhachithecium (1)
 Family **Rhabdoweisiaceae**
Oreoweisia (1)
 ORDER POTTIALES
 Family **Pottiaceae**
Anoetangium (3)
Barbula (6)
Bryoerythrophyllum (1)
Chionoloma (1)
Didymodon (1)
Gymnostomiella (1)
Gymnostomum (1)
Hymenostylium (1)
Hyophila (7)
Leptodontium (3)
Splachnobryum (2)
Streptopogon (2)
Tortella (1)
Tortula (4)
Trichostomum (6)
Weisiopsis (1)
Weissia (1)
 Family **Serpotortellaceae**
Serpotortella (2)
 SUBCLASS BRYIDAE
 Super order **Bryanae**
 ORDER SPLACHNALES
 Family **Meesiaceae**
Lepiobryum (1)
 Family **Splachnaceae**
Brachymitrium (1)
Tayloria (4)
 ORDER BRYALES
 Family **Bryaceae**
Anomobryum (2)
Brachymerium (12)
Bryum (26)
Mniobryum (1)
Rhodobryum (3)
 Family **Mniaceae**
Epipterygium (1)
Mielichhoferia (2)
Plagiomnium (1)
Pohlia (4)
Pseudopohlia (1)
Schizymerium (2)
 ORDER BARTRAMIALES
 Family **Bartramiaceae**
Bartramia (2)
Breutelia (8)
Philonotis (7)
 ORDER ORTHOTRICHALES
 Family **Orthotrichaceae**
Cardotiella (4)
Groutiella (1)
Macrocoma (1)
Macromitrium (24)
Schlotheimia (31)
Ulota (1)
Zygodon (4)
 ORDER HEDWIGIALES
 Family **Hedwigiaceae**
Braunia (1)
Bryowijkia (1)
Hedwigia (1)
 Family **Rhacocarpaceae**
Rhacocarpus (1)
 ORDER RHIZOGONIALES
 Family **Rhizogoniaceae**
Pyrrhobryum (1)
 Seper order **Hypnanae**
 ORDER HYPNODENDRALES
 Family **Racopilaceae**
Powellia (2)
Racopilum (10)
 ORDER HOOKERIALES
 Family **Daltoniaceae**
Adelothecium (1)
Calyptrochaeta (1)
Daltonia (5)
Distichophyllum (2)
 Family **Hypopterygiaceae**
Hypopterygium (1)
Lopidium (1)
 Family **Leucomiaceae**
Leucomium (1)
 Family **Pilotrichaceae**
Callicostella (13)
Cyclodictyon (3)
Hookeriopsis (1)
Lepidopilidium (5)
Lepidopilum (3)
 ORDER HYPNALES
 Family **Amblystegiaceae**
Amblystegium (2)
Hygrohypnum (1)

- Family **Anomodontaceae**
Herpetineuron (1)
- Family **Brachytheciaceae**
Aerolindigia (1)
Brachythecium (2)
Eurhynchium (2)
Helicodontium (1)
Palamocladium (1)
Rhynchostegiella (1)
Rhynchostegium (5)
Schimperella (1)
Squamidium (1)
- Family **Catagoniaceae**
Catagonium (1)
- Family **Cryphaeaceae**
Cryphaea (2)
Schoenobryum (1)
- Family **Entodontaceae**
Campylodontium (1)
Entodon (5)
Erythrodontium (1)
Mesonodon (1)
- Family **Fabroniaceae**
Fabronia (8)
Rhizofabronia (1)
- Family **Hypnaceae**
Ectropothecium (12)
Gammiella (1)
Glossadelphus (3)
Hypnum (2)
Mittenothamnium (7)
Phyllodon (2)
Rhacopilopsis (2)
Taxiphyllum (1)
Vesicularia (9)
- Family **Leptodontaceae**
Leptodon (1)
- Family **Leskeaceae**
Pseudoleskea (1)
- Family **Leucodontaceae**
Leucodon (2)
Pterogoniadelphus (1)
Pterogonium (2)
- Family **Meteoriaceae**
Aerobryopsis (1)
Barbella (1)
Floribundaria (4)
Papillaria (5)
Trachypodopsis (1)
Trachypus (2)
- Family **Neckeraceae**
Homaliodendron (2)
- Neckera* (2)
Neckeropsis (4)
Orthostichella (5)
Pilotrichella (4)
Pinnatella (1)
Porotrichum (5)
Thamnobryum (1)
- Family **Phyllogoniaceae**
Phyllogonium (1)
- Family **Prionodontaceae**
Prionodon (1)
- Family **Pterignandraceae**
Trachyphyllum (2)
- Family **Pterobryaceae**
Calyptothecium (2)
Hildebrandtiella (3)
Jaegerina (2)
Orthostichidium (1)
Orthostichopsis (5)
Pterobryopsis (1)
Renaudia (3)
- Family **Pylaisiadelphaceae**
Isopterygium (14)
Taxithelium (7)
Wijkia (4)
- Family **Regmatodontaceae**
Regmatodon (1)
- Family **Rigodiaceae**
Rigodium (1)
- Family **Rutenbergiaceae**
Rutenbergia (5)
- Family **Sematophyllaceae**
Acanthorrhynchium (1)
Acroporium (5)
Clastobryophilum (1)
Macrohymenium (4)
Meiothecium (3)
Radulina (1)
Rhaphidorrhynchium (3)
Sematophyllum (11)
Trichosteleum (10)
Warburgiella (1)
- Family **Stereophyllaceae**
Entodontopsis (2)
Stereophyllum (1)
- Family **Symphodontaceae**
Symphodon (1)
- Family **Thuidiaceae**
Pelekium (7)
Raiiella (1)
Thuidium (3)

Liverworts reported from Madagascar

Adelanthaceae*Adelanthus decipiens* (Hook.) Mitt. (Pócs & Geissler, 2002)*Adelanthus lindenbergianus* (Lehm.) Mitt. (Grolle, 1995)**Aneuraceae**

**Aneura pseudopinguis* (Herzog) Pócs – Ambavaniasy, réserve de Vohimana, bois mort oblique en décomposition, alt. 849 m, S 18°55'43.6" E 48°29'56.6", 15/04/2010, Reeb, *Andriamananatena & Bidault CRAE 106*, TAN, det. Reeb & Andriamananatena; Ambavaniasy, réserve de Vohimana, forêt ombrophile, tronc vertical d'arbre vivant, alt. 830 m, S 18°55'09.33" E 48°30'49.0", 16/04/2010, Reeb, *Andriamananatena & Bidault CRAE120* TAN, det. Reeb & Andriamananatena; Anjangoveratra, forêt du Makirovana, forêt ombrophile dense orientale, au dessus d'arbre mort horizontal, alt. 432 m, S 14°10'13.9" E 49°57'12.9", 04/05/2010, Reeb CR220, TAN, det. Reeb.

Riccardia amazonica (Spruce) Schiffn. ex Gradst. (Pócs & Geissler, 2002)*Riccardia erosa* (Steph.) E.W. Jones (Pócs & Geissler, 2002)*Riccardia longispica* (Steph.) Pearson (Grolle, 1995; Pócs & Geissler, 2002)*Riccardia multifida* (L.) Gray (Grolle, 1995)*Riccardia nudiflora* (Steph.) Grolle (Grolle, 1995)*Riccardia saccatiflora* (Steph.) S.W. Arnell (Grolle, 1995)*Riccardia* sp. (*Aneura caespitans* Steph.) (Grolle, 1995)*Riccardia* sp. (*Aneura corbieri* Steph.) (Grolle, 1995)*Riccardia* sp. (*Aneura dismieri* Steph.) (Grolle, 1995)**Arnellaceae***Gongylanthus ericetorum* (Raddi) Nees (Grolle, 1995)**Aytoniaceae***Asterella coronata* (Steph.) H.A. Mill. (Grolle, 1995)*Asterella wilmsii* (Steph.) S.W. Arnell (Grolle, 1995)*Plagiochasma microcephalum* (Steph.) Steph. (Grolle, 1995)**Balantiopsidaceae***Isotachis aubertii* (Schwaegr.) Mitt. (Grolle, 1995; Pócs & Geissler, 2002)**Calypogeiaceae***Calypogeia annabonensis* Steph. (Pócs & Geissler, 2002)*Calypogeia arguta* Nees & Mont. (Grolle, 1995)*Calypogeia bidentula* (F. Weber) Nees (Grolle, 1995)**Calypogeia fissa* (L.) Raddi – Ankaratra, sur sol, alt. 2000 m, 27/03/1972, *Cremers 1947*, TAN.*Calypogeia longifolia* Steph. (Grolle, 1995; Pócs, 2005)*Calypogeia mascarenensis* Bischl. (Grolle, 1995)*Calypogeia microstipula* (Steph.) Steph. (Grolle, 1995)*Mnioloma fuscum* (Lehm.) R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)

Cephaloziaceae

Cephalozia connivens (Dicks.) Lindb. subsp. *fissa* Vána (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)

Iwatsukia jishibae (Steph.) N. Kitag. (Pócs, 1995; Pócs & Geissler, 2002)

Cephaloziellaceae

Amphicephalozia geisslerae Pócs & Vána (Pócs & Vána, 2001; Pócs & Geissler, 2002) **End**, Type – Antsiranana, Manongarivo Special Reserve, NW Madagascar, alt. 1300-1350 m, 10/03/1999, *Geissler 19708/3*, holotype G, paratype EGR, G, PRC.

Cephaloziella kiaeri (Austin) S.W. Arnell (Grolle, 1995; Pócs & Geissler, 2002)

Cephaloziella sp. (Grolle, 1995)

Cylindrocolea atroviridis (Sim) Vána (Grolle, 1995)

Cylindrocolea madagascariensis (Steph.) R.M. Schust. (Grolle, 1995) **End**, Type – Imerina, *Hildebrandt*, herb (N.S.).

Kymatocalyx dominicensis (Spruce) Vána (Gradstein & Vána, 1999)

Kymatocalyx madagascariensis (Steph.) Gradst. & Vána (Grolle, 1995; Pócs, 1995; Gradstein & Vána, 1999; Pócs & Geissler, 2002)

Kymatocalyx rhizomatica (Herzog) Gradst. & Vána (Pócs & Geissler, 2002)

Cyathodiaceae

Cyathodium africanum Mitt. (Pócs & Geissler, 2002)

Dumortieraceae

**Dumortiera hirsuta* (Sw.) Nees – Anjozorobe, forêt ombrophile d'altitude, sur des terres humides, 02/1959, *Bosser 12648*, TAN; Marojejy National Park, Talus terreux ombragé, alt. 690 m, S 14°26'07.8" E 49°45'49.9", 27/11/2009, *Ah-Peng 349*, det. Ah-Peng; Ambavaniasy, réserve de Vohimana, forêt ombrophile d'altitude, au pied d'une cascade, alt. 849 m, S 18°55'43.6" E 48°29' 56.6" 15/04/2010, *Reeb, Andriamananatenana & Bidault CRAE93*, TAN, det. Reeb; Anjangoveratra, forêt du Makirovana, sur falaise suintante, alt. 508 m, S 14°10'17.4" E 49°57'07.5", 07/05/2010, *Reeb CR302*, TAN, det. Reeb.

Fossombroniaceae

Fossombronia sp. (Pócs & Geissler, 2002)

Frullaniaceae

Frullania anderssonii Aongstr. (Grolle, 1995)

Frullania angulata Mitt. var. *angulata* (Grolle, 1995; Pócs & Geissler, 2002)

Frullania angulata var. *laciniata* Demaret *et* Vanden Berghen (Grolle, 1995)

Frullania apicalis Mitt. (Grolle, 1995; Pócs & Geissler, 2002)

Frullania apiculata (Reinw. *et al.*) Nees (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)

Frullania arecae (Spreng.) Gottsche (Grolle, 1995)

Frullania borbonica Lindenb. (Grolle, 1995)

Frullania bullata Steph. (Grolle, 1995)

Frullania caffraria Steph. (Grolle, 1995)

Frullania capensis Gottsche (Grolle, 1995)

Frullania depressa Mitt. (Grolle, 1995)

Frullania diptera (Lehm.) Drège (Grolle, 1995)

- **Frullania ecklonii* (Spreng.) Gottsche *et al.* – Ambatovory, Tananarive, vestige de forêt, sur un tronc d'arbre, 04/1957, *Bosser 11021*, TAN.
- Frullania ericoides* (Nees) Mont. (Grolle, 1995)
- Frullania gabonensis* Vanden Berghen (Grolle, 1995; Pócs, 1995)
- Frullania grossiclava* Steph. (Grolle, 1995; Pócs, 1995; Grolle, 2001; Pócs & Geissler, 2002)
- Frullania humbertii* Vanden Berghen (Grolle, 1995)
- Frullania imerinensis* Steph. (Grolle, 1995; Pócs & Geissler, 2002)
- Frullania lindenberghii* Lehm. (Grolle, 1995; Pócs, 1995; Grolle, 2001; Pócs & Geissler, 2002)
- Frullania longistipula* Steph. (Grolle, 1995) **End**, Type – Imerina, Ankadivavala, *Camboué 162*, holotype G.
- Frullania loricata* Pearson (Grolle, 1995; Pócs & Geissler, 2002)
- Frullania loricata* var. *laxa* Pearson (Grolle, 1995) **End**, Type – unknown.
- Frullania nodulosa* (Reinw. *et al.*) Gottsche *et al.* var. *nodulosa* (Grolle, 1995; Pócs, 1995)
- Frullania obscurifolia* Mitt. (Grolle, 1995; Pócs, 1995)
- Frullania purpurea* Steph. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
- Frullania repandistipula* Sande Lac. (Grolle, 1995)
- Frullania rigida* Steph. (Grolle, 1995) **End**, Type – unknown.
- Frullania schimperi* var. *laciniata* Vanden Berghen (Grolle, 1995) **End**, Type – *Onraedt 74M8078c*, holotype BR.
- Frullania schimperi* Nees var. *schimperi* (Grolle, 1995; Pócs & Geissler, 2002)
- Frullania serrata* var. *pertenuis* (Nees) Gottsche *et al.* (Grolle, 1995; Pócs, 1995)
- Frullania serrata* Gottsche var. *serrata* (Grolle, 1995)
- Frullania socotrana* Mitt. (Grolle, 1995)
- Frullania spongiosa* Steph. (Grolle, 1995; Pócs, 1995)
- Frullania trinervis* (Lehm.) Drège (Grolle, 1995)
- Frullania usambarana* Schiffn. *ex* Steph. (Grolle, 1995; Pócs, 1995)
- Frullania usambarana* var. *reducta* Vanden Berghen (Grolle, 1995)
- Frullania vanden-berghenii* Pócs (Grolle, 1995; Pócs, 1995)
- Frullania variegata* Steph. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
- Herbertaceae**
- Herbertus dicranus* (Taylor *ex* Gottsche *et al.*) Trevis. (Grolle, 1995; Pócs, 1995; Grolle, 2001; Hodgetts, 2008)
- Herbertus juniperoideus* (Sw.) Grolle (Grolle, 1995; Grolle, 2001; Pócs & Geissler, 2002; Hodgetts, 2008)
- Jamesoniellaceae**
- Cryptochila grandiflora* (Lindenb. *et* Gottsche) Grolle (Grolle, 1995)
- Cuspidatula contracta* (Reinw. *et al.*) Steph. (Pócs, 1995)
- Denotarisia linguifolia* (De Not.) Grolle (Pócs & Geissler, 2002)
- Syzygiella purpurascens* (Steph) Feldberg *et al.* (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
- Syzygiella concreta* (Gottsche) Spruce (Grolle, 1995; Pócs & Geissler, 2002)
- Syzygiella geminifolia* (Mitt.) Steph. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)

Jungermanniaceae

Gottschelia schizopleura (Spruce) Grolle (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)

Notoscyphus lutescens (Lehm. *et* Lindenb.) Mitt. (Grolle, 1995; Pócs & Geissler, 2002)

Solenostoma borgenii (Gottsche) Steph. (Grolle, 1995)

Solenostoma onraedtii (Vàña) Vàña *et al.* (Grolle, 1995)

Solenostoma renauldii (Vàña) Vàña *et al.* (Grolle, 1995)

Solenostoma sphaerocarpum (Hook.) Steph. (Grolle, 1995)

Lejeuneaceae

Acanthocoleus aberrans (Lindenb. *et* Gottsche) Kruijt (Kruijt, 1988; Grolle, 1995)

Acanthocoleus madagascariensis (Steph.) Kruijt (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)

Acrolejeunea aulacophora (Mont.) Steph. (Grolle, 1995)

Acrolejeunea emergens (Mitt.) Steph. var. *emergens* (Grolle, 1995; Pócs & Geissler, 2002)

Acrolejeunea pycnolada (Taylor) Schiffn. (Grolle, 1995)

Archilejeunea alata Steph. (Grolle, 1995)

Archilejeunea brevilobula Steph. (Grolle, 1995) **End**, Type – Oriental coast, Sakara, holotype G.

Archilejeunea helenae Pócs *et* Gyarmati (Pócs & Sass-Gyarmati, 2006) **End**, Type – Mananara-Nord Biosphere Reserve, lowland rainforest on the East slopes of Mahavoho Hill, epiphyllous on relatively rigid leathery leaf, alt. 250-350 m, S 16°27' E 49°46.9-47.5', 14-16/08/1998, Pócs & Szabó 9878/FM, holotype EGR.

Archilejeunea nobilis (Gottsche) Steph. (Grolle, 1995) **End**, Type – unknown.

Brachiolejeunea phyllorhiza (Nees) Kruijt *et* Gradst. (Grolle, 1995)

Bryopteris gaudichaudii Gottsche (Grolle, 1995; Pócs, 1995)

Caudalejeunea grolleana Gradst. (Grolle, 1995) **End**, Type – Nosy Be, Lokobe natural reserve, on bark in primary forest, alt. 100 m, 15/07/1971, *Onraedt M5119*, holotype BR, isotype JE.

Caudalejeunea hanningtonii (Mitt.) Schiffn. (Grolle, 1995)

Caudalejeunea lewallei Vanden Berghen (Grolle, 1995)

Caudalejeunea recurvistipula (Gottsche) Schiffn (Grolle, 1995)

Ceratolejeunea andringitrae Pócs (Pócs, 2011a) **End**, Type – Ihorombe Region in former Fianarantsoa Province, Andringitra National Park, Montane rainforest on the West side of Korokoro River, around Camp II, epiphyll, alt. 750-1000 m, S 22°13' E 47°1-2', 20-23/09/1994, Pócs & A. Szabó 9472/AF, holotype EGR, isotypes MO, TAN.

Ceratolejeunea belangeriana (Gottsche) Steph. (Bonner, 1953; Grolle, 1995; Pócs & Geissler, 2002; Pócs, 2011a)

Ceratolejeunea diversicornua Steph. (Pócs, 2011a)

Ceratolejeunea cornuta (Lindenb.) Schiffn. (Grolle, 1995; Pócs, 2011a)

Ceratolejeunea papuliflora Steph. (Bonner, 1953; Grolle, 1995; Pócs, 2011a)

Ceratolejeunea saroltae Pócs (Pócs, 2011a) **End**, Type – Toamasina Province, Maromizaha forest, Mossy montane rainforest with bamboo (*Nastus* sp.), undergrowth on the summit ridge of Mt. Maromizaha, south of the Andasibe National Park, on twigs, alt. 1080-1214 m, *Sarolta Pócs 9890/BJ*, 26/09/1998, holotype EGR, paratype EGR.

- Cheilolejeunea cordigera* (Steph.) Grolle (Grolle, 1995; Pócs & Geissler, 2002)
- Cheilolejeunea cordistipula* (Steph.) Grolle ex E.W. Jones (Grolle, 1995; Malombe, 2007)
- Cheilolejeunea decursiva* (Sande Lac.) R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002; Malombe, 2007)
- Cheilolejeunea intertexta* (Lindenb.) Steph. (Grolle, 1995; Pócs & Geissler, 2002; Malombe, 2007)
- Cheilolejeunea krakakammae* (Lindenb.) R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002; Malombe, 2007)
- Cheilolejeunea montagnei* (Gottsche) R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002; Malombe, 2007)
- Cheilolejeunea pluriplicata* (Pearson) R.M. Schust. (Grolle, 1995; Malombe, 2007)
- Cheilolejeunea pocsii* E.W. Jones (Grolle, 1995; Malombe, 2007)
- Cheilolejeunea serpentina* (Mitt.) Mizut. (Grolle, 1979; Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002; Malombe, 2007)
- Cheilolejeunea surrepens* (Mitt.) E.W. Jones (Grolle, 1995; Pócs & Geissler, 2002)
- Cheilolejeunea trapezia* (Nees) Kachroo et R.M. Schust. (Malombe, 2007)
- Cheilolejeunea trifaria* (Reinw. et al.) Mizut. (Grolle, 1995; Pócs & Geissler, 2002)
- Cheilolejeunea usambarana* (Steph.) Grolle (Malombe, 2007)
- Cheilolejeunea xanthocarpa* (Lehm. & Lindenb.) Malombe (Pócs, 1995; Malombe, 2007)
- Cololejeunea adnata* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Tamatave, Foulpointe, forêt d'Analalava, alt. 100 m, 05/12/1975, *Tixier 7637*, holotype PC.
- Cololejeunea andapania* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Diégo-Suarez, massif de l'Anjanaharibe, Ouest d'Andapa, Haute Andramota, bassin de la rivière Lokoho, forêt ombrophile sur gneiss et granite, alt. 700 m, 10/12/1950, *Humbert, Capuron & Cour 1/E*, holotype PC.
- Cololejeunea androphylla* var. *madecassa* Tixier (Grolle, 1995) **End**, Type – Antananarive, Mandialaza, alt. 1200 m, *Tixier 7670*, holotype PC.
- Cololejeunea ankaiana* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Route de Tamatave, Moramanga - Anosibeana, alt. 1000 m, 18/4/1978, *Tixier s.n.*, holotype PC.
- Cololejeunea appressa* (A. Evans) Benedix (Grolle, 1995; Pócs & Geissler, 2002)
- Cololejeunea auriculata* (E.W. Jones) R.M. Schust. (Tixier, 1985; Grolle, 1995; Pócs & Geissler, 2002)
- Cololejeunea bidentula* (Steph.) E.W. Jones (Grolle, 1995)
- Cololejeunea bolombensis* (Steph.) Vanden Berghen (Tixier, 1985; Grolle, 1995; Pócs & Geissler, 2002)
- Cololejeunea borbonica* Tixier (Grolle, 1995)
- Cololejeunea camusii* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Antananarivo, Ambatoloana, Andasibe, alt. 1200 m, 10/11/1976, *Tixier 9593*, holotype PC.
- Cololejeunea capuronii* Tixier (Grolle, 1995) **End**, Type – Massif de l'Anjanaharibe, à l'Ouest d'Andapa, Andramonta (pente et sommet nord), alt. 500-700 m, *Humbert, Capuron & Cours s.n.*, holotype PC.
- Cololejeunea cardiocarpa* (Mont.) A. Evans (Tixier, 1985; Grolle, 1995)
- Cololejeunea cristata* (Steph.) R.M. Schust. (Tixier, 1985; Grolle, 1995)

- Cololejeunea cuneata* (Lehm. *et* Lindenb.) Herzog (Grolle, 1995; Pócs, 1995)
Cololejeunea decemplicata (Steph.) Tixier (Grolle, 1995)
Cololejeunea deroinii Tixier (Tixier, 1993; Grolle, 1995) **End**, Type – Diégo-Suarez (Antsiranana), Massif du Marojejy, rive gauche de la rivière Manantenina, alt. 350 m, *Deroïn & Badré 5*, holotype PC.
Cololejeunea diplasiolejeuneoides Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Tamatave, Périnet, forêt d'Antaniditra, alt. 950 m, 6/7/1977, *Tixier 10637*, holotype PC.
Cololejeunea disciflora Tixier (Grolle, 1995) **End**, Type – Antananarivo, Carion, Angavobe, alt. 1600 m, *Tixier 10834*, holotype PC.
Cololejeunea distalopapillata (E.W. Jones) R.M. Schust. (Tixier, 1985; Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea dolichodonta Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Fianarantsoa, Ambatofinandrahana, alt. 1650 m, 21/3/1978, *Tixier 11394*, holotype PC.
Cololejeunea duvignaudii E.W. Jones (Tixier, 1985; Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea duvignaudii var. *papillata* Tixier (Grolle, 1995)
Cololejeunea elegans Steph. (Tixier, 1985; Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea falcata var. *madecassa* Tixier (Grolle, 1995) **End**, Type – Tamatave, Périnet, alt. 917 m, *Tixier 10160*, holotype PC.
Cololejeunea floccosa (Lehm. *et* Lindenb.) Schiffn. (Grolle, 1995)
Cololejeunea floccosa var. *trivittata* Tixier (Grolle, 1995)
Cololejeunea furcibulata (Berrie *et* E.W. Jones) R.M. Schust. (Grolle, 1995)
Cololejeunea hildebrandii (Austin) Steph. (Tixier, 1985; Grolle, 1995)
Cololejeunea leloutrei (E.W. Jones) R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea leloutrei var. *microlobulata* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Tananarive, Ambatolampy, station de Manjakatempo, alt. 1700 m, 27/10/1976, *Tixier 9385*, holotype PC.
Cololejeunea leloutrei var. *ugulurica* Pócs *ex* Tixier (Grolle, 1995)
Cololejeunea lemuriana Tixier (Tixier, 1985; Grolle, 1995)
Cololejeunea marginata (Lehm. *et* Lindenb.) Schiffn. (Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea microscopica (Taylor) Schiffn. var. *exigua* (A. Evans) Bernecker *et* Pócs (Grolle, 1995; Pócs & Bernecker, 2009)
Cololejeunea minutissima (Sm.) Schiffn. (Grolle, 1995)
Cololejeunea moramangae Tixier (Grolle, 1995; Pócs & Bernecker, 2009)
Cololejeunea mocambiquensis S.W. Arnell (Grolle, 1995)
Cololejeunea obliqua (Nees *et* Mont.) Schiffn. (Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea obtusifolia (E.W. Jones) Tixier (Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea peraffinis var. *serrulata* Benedix (Pócs & Geissler, 2002)
Cololejeunea plagiochiliana Tixier (Grolle, 1995) **End**, Type – Périnet, *Benoist s.n.*, holotype PC.
Cololejeunea platyneura (Spruce) A. Evans (Grolle, 1995; Pócs & Geissler, 2002)
Cololejeunea praeruptorum Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Mandialaza, forêt de l'Angavo, 19/12/1975, *Tixier 7670*, holotype PC.

- Cololejeunea pteroporum* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Diégo-Suarez, station de roussettes, alt. 900 m, 06/11/1975, *Tixier 7463*, holotype PC.
- Cololejeunea raduliloba* Steph. (Tixier, 1985; Grolle, 1995)
- Cololejeunea saltuum* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Fianarantsoa, Ranomafana, forêt du pk 24, alt. 1200 m, 30/12/1976, *Tixier 10038*, holotype PC.
- Cololejeunea sambiroana* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Sambirano, forêt d'Anjozobe, alt. 300m, 22/08/1977, *Tixier 10744*, holotype PC.
- Cololejeunea selangorensis* Tixier (Tixier, 1985; Grolle, 1995)
- Cololejeunea subinflata* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Antananarivo, Manjakandriana, lac Mantasoa, 19/04/1979, *Tixier 8158*, holotype PC.
- Cololejeunea succinea* Tixier (Tixier, 1985; Tixier, 1979a) **End**, Type – Diégo-Suarez, Montagne d'Ambre, station des Roussettes, forêt de montagne, 03/11/1975, *Tixier 7395*, holotype PC.
- Cololejeunea tamatavensis* Tixier (Tixier, 1985; Grolle, 1995) **End**, Type – Foulpointe, forêt d'Analalava, alt. 100 m, 05/12/1975, *Tixier 7230*, holotype PC.
- Cololejeunea tanzaniae* Pócs (Grolle, 1995; Pócs & Geissler, 2002)
- Cololejeunea vidaliana* Tixier (Grolle, 1995)
- Cololejeunea zenkeri* (Steph.) E.W. Jones (Pócs & Geissler, 2002)
- Colura benoistii* Jovet-Ast (Grolle, 1995)
- Colura bicornis* Jovet-Ast (Grolle, 1995; Pócs, 1995) **End**, Type – Route de Moramanga à Anosibe, pk 29, forêt marécageuse, sur feuille de palmier, 15/09/1953, *Millot & Bosser 6319*, herb (N.S.)
- Colura digitalis* (Mitt.) Steph. (Pócs, 1995; Pócs & Geissler, 2002)
- Colura heimii* Jovet-Ast (Grolle, 1995)
- Colura humbertii* Jovet-Ast (Grolle, 1995)
- Colura inornata* Jovet-Ast (Grolle, 1995; Pócs, 1995) **End**, Type – Route de Moramanga à Anosibe, pk 29, forêt marécageuse, sur feuille de palmier, 15/09/1953, *Millot & Bosser 6323*, herb (N.S.)
- Colura obesa* Jovet-Ast (Grolle, 1995)
- Colura obvoluta* Jovet-Ast (Jovet-Ast, 1983; Grolle, 1995)
- Colura tenuicornis* (A. Evans) Steph. (Grolle, 1995)
- Diplasiolejeunea andringitrae* Pócs et Schafer-Verwimp (Pócs & Schaefer-Verwimp, 2006) **End**, Type – Monts d'Andringitra, Nature Reserve, montane rainforest, West side of Korokoro River, around Camp II, alt. 750-1000 m, S 22°13' E 47°1-2', 20-23/9/1994, *Pócs et al., 9472/AM*, holotype EGR.
- Diplasiolejeunea aulae* E.W. Jones (Grolle, 1995)
- Diplasiolejeunea auriculata* Tixier (Grolle, 1995) **End**, Type – Fianarantsoa, forêt de Tsarafidy, *Tixier 8908*, holotype PC.
- Diplasiolejeunea cavifolia* Steph. (Grolle, 1995; Pócs & Geissler, 2002)
- Diplasiolejeunea cobrensis* Gottsche ex Steph. (Grolle, 1995; Pócs & Geissler, 2002)
- Diplasiolejeunea cobrensis* Pócs subsp. *antsirananae* (Pócs, 2001; Pócs & Geissler, 2002) **End**, Type – Province d'Antsiranana, Réserve Spéciale de

Manongarivo, on the rain forest covered north ridge leading to the 1869 m high summit of Manongarivo massif, epiphyllous, alt. 850-950 m, N 13°59' E 48°26', 3/1999, *Geissler 19549/8*, holotype G.

- Diplasiolejeunea comorensis* Tixier (Grolle, 1995)
Diplasiolejeunea cornuta Steph. (Grolle, 1995; Pócs, 1995)
Diplasiolejeunea ensifera Tixier (Grolle, 1995) **End**, Type – Antananarivo, Andasibe, alt. 1400 m, *Tixier 9626*, holotype PC.
Diplasiolejeunea hamata Tixier (Grolle, 1995) **End**, Type – Fianarantsoa, Vohiparara, *Tixier 11373*, holotype PC.
Diplasiolejeunea insignis Tixier (Grolle, 1995) **End**, Type – Tananarive, Carion, Angavokely, alt. 1800 m, 27/01/1977, *Tixier 10258*, holotype PC.
Diplasiolejeunea jonesii Tixier (Grolle, 1995) **End**, Type – Tamatave, Antaniditra, Vohiparara, alt. 1100 m, 30/12/1976, *Tixier 10157*, holotype PC.
Diplasiolejeunea kraussiana (Lindenb.) Steph. (Grolle, 1995)
Diplasiolejeunea lemuriana Tixier (Grolle, 1995) **End**, Type – Fianarantsoa, Ranomafana, alt. 1200 m, 30/12/1976, *Tixier 10171*, holotype PC.
Diplasiolejeunea magnistipulata Tixier (Tixier, 1985; Grolle, 1995)
Diplasiolejeunea ornata Pócs *et* Schäfer-Verwimp (Pócs & Schaefer-Verwimp, 2006) **End**, Type – Province de Toamasina, Mananara - Nord Biosphere Reserve, Lowland rain forest on the NW slope of Behafotra Hill, alt. 250-300 m, S 16°27.2' E 49°47.7', 16/08/1998, *Pócs & Szabó 9877/CH*, holotype EGR.
Diplasiolejeunea palustrium Tixier (Grolle, 1995) **End**, Type – Tamatave, Périnet, Antaniditra, alt. 1000 m, 06/07/1977, *Tixier 10636*, holotype PC.
Diplasiolejeunea phyllarthonii Tixier (Grolle, 1995) **End**, Type – Tamatave, Manohitaly (route du Chrome), alt. 1200 m, 03/03/1978, *Tixier 11632*, holotype PC.
Diplasiolejeunea ramicola Tixier (Grolle, 1995) **End**, Type – Antananarivo, Ambatoloana, 1400 m, *Tixier 9629*, holotype PC.
Diplasiolejeunea ranomafanae Pócs & Schäfer-Verwimp (Pócs & Schaefer-Verwimp, 2006) **End**, Type – Ranomafana National Park, on the summit ridge of Mont Vatolampy near the telecom aerial, 2.3 km W of Ambatolahy village, alt. 1200 m, S 21°15.10' E 47°24.44', 30/07/2004, *Pócs 04128/AK*, holotype EGR.
Diplasiolejeunea runssorensis Steph. (Grolle, 1995)
Diplasiolejeunea subcornuta Tixier (Grolle, 1995)
Diplasiolejeunea symoensii Vanden Berghen (Grolle, 1995)
Diplasiolejeunea utriculata Steph. (Grolle, 1995)
Diplasiolejeunea villaumei Steph. (Grolle, 1995)
Diplasiolejeunea zakiae Tixier (Tixier, 1977; Pócs & Geissler, 2002)
Drepanolejeunea cambouena Steph. (Grolle, 1995; Pócs, 2011b)
Drepanolejeunea cultrella (Mitt.) Steph. (Pócs & Geissler, 2002)
Drepanolejeunea geisslerae Pócs (Pócs, 2001; Pócs & Geissler, 2002) **End**, Type – Antsiranana, Réserve Spéciale de Manongarivo, NW Madagascar, abundant on palm stem, alt. 950-1050 m, N 13°59' E 48°26', 03/1999, *Geissler 19559*, holotype G.
Drepanolejeunea madagascariensis (Steph.) Grolle (Grolle, 2001; Pócs & Geissler, 2002)

- Drepanolejeunea mascarena* (S.W. Arnell) R.L. Zhu *et* Grolle (Zhu & Grolle, 2003)
- Drepanolejeunea pentadactyla* (Mont.) Steph. (Mizutani, 1975; Pócs, 2011b)
- Drepanolejeunea physaefolia* (Gottsche) Steph. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
- Drepanolejeunea pocsii* Grolle (Pócs & Geissler, 2002)
- Drepanolejeunea trematodes* (Nees) Bischl. (Grolle, 1995; Pócs & Geissler, 2002)
- Frullanooides tristis* (Steph.) Van Slageren (Grolle, 1995)
- Haplolejeunea sticta* Grolle (Grolle, 1995; Pócs & Geissler, 2002)
- Lejeunea alata* Gottsche (Grolle, 1995; Pócs & Geissler, 2002)
- Lejeunea alata* var. *patriciae* Pócs (Pócs, 2001; Pócs & Geissler, 2002) **End**, Type – Province d’Antsiranana, Réserve Spéciale de Manongarivo, on the rain forest covered north ridge leading to the 1869 m high summit of Manongarivo massif, epiphyllous, N 13°59' E 48°26', 12/03/1999, *Geissler 19856/I*, holotype G.
- Lejeunea amaniensis* E.W. Jones (Grolle, 1995)
- Lejeunea anisophylla* Mont. (Grolle, 1985; Pócs & Geissler, 2002; Pócs, 2011b)
- Lejeunea capensis* Gottsche (Grolle, 1995)
- Lejeunea confusa* E.W. Jones (Pócs & Geissler, 2002)
- Lejeunea ecarinata* (Steph.) Steph. (Grolle, 1995)
- Lejeunea eckloniana* Lindenb. (Grolle, 1995; Pócs & Geissler, 2002)
- Lejeunea flava* (Sw.) Nees (Grolle, 1995)
- Lejeunea flavovirens* Aongstr. (Grolle, 1995; Pócs & Geissler, 2002)
- Lejeunea isophylla* E.W. Jones (Grolle, 1995)
- Lejeunea julacea* Steph. (Grolle, 1995; Pócs, 2011b) **End**, Type – *Forsyth-Major B 473*, holotype G.
- Lejeunea leucosis* Besch. & Spruce (Grolle, 1995; Pócs, 2010a)
- Lejeunea masoalae* Pócs (Pócs, 2010a) **End**, Type – West side of Masoala Peninsula, above Antongil Bay, montane rainforest on the summit ridge SE of Ambanizana village, alt. 660-720 m, S 15°37' E 50°05', 09/09/1994, *Pócs 9448/AN*, holotype EGR, isotype MO, TAN.
- Lejeunea obtusata* Gottsche (Grolle, 1995)
- Lejeunea papilionacea* Steph. (Grolle, 1995; Zhu & Grolle, 2001)
- Lejeunea phyllobola* Nees *et* Mont. (Pócs, 1995)
- Lejeunea tabularis* (Spreng.) Gottsche *et al.* (Grolle, 1995; Pócs & Geissler, 2002)
- Lejeunea tuberculosa* Steph. (Grolle, 1995; Pócs & Geissler, 2002)
- Lejeunea villaumei* (Steph.) Grolle (Grolle, 1995; Pócs & Geissler, 2002)
- Lejeunea vojtkoi* Pócs (Pócs, 2010a) **End**, Type – 10 km North of Fianarantsoa, on decaying wood in montane forest, alt. 1230-1360 m, S 21°15' E 47°14', 22/09/1994, *Vojtkó 9461/AY*, holotype EGR.
- Lejeunea vulgariformis* Gottsche (Grolle, 1995; Pócs, 2010a)
- Lepidolejeunea bidentula* (Steph.) R.M. Schust. var. *bidentula* (Piippo, 1986; Grolle, 1995; Zhu & So, 2001)
- Leptolejeunea epiphylla* (Mitt.) Steph. (Pócs & Geissler, 2002)
- **Leptolejeunea vitrea* (Nees) Schiffn. – Anjozorobe, épiphyllous, alt. 300 m, 22/07/1977, *Tixier 10743*, TAN.
- Lopholejeunea borbonica* Steph. (Grolle 1995, Pócs & Geissler, 2002)
- Lopholejeunea erugata* B. Thiers (Grolle, 1995) **End**, Type – 1896, *Forsyth-Major*, holotype G.

- Lopholejeunea eulopha* (Taylor) Schiffn. (Grolle, 1995; Pócs & Geissler, 2002; Zhu & Gradstein, 2005)
- Lopholejeunea grandicrista* Steph. (Grolle, 1995; Pócs & Geissler, 2002)
- Lopholejeunea leioptera* Gyarmati (Sass-Gyarmati, 2001; Pócs & Geissler, 2002) **End**, Type – Fianarantsoa, alt. 1590 m, S 22°11'00" E 46°53'00", 19/09/1994, Magill & Pócs 12855, holotype MO.
- Lopholejeunea lepidoscypha* Kiaer *et* Pearson (Grolle, 1995) **End**, Type – Ankaratra, 1877, *Borgen s.n.*, holotype BM.
- Lopholejeunea multilacera* Steph. (Grolle 1995)
- Lopholejeunea nigricans* (Lindenb.) Schiffn. (Grolle, 2001; Zhu & Gradstein, 2005)
- Lopholejeunea onraedtii* Vanden Berghen (Grolle, 2001) **End**, Type – Route de Moramanga, Tamatave, 17 km from Moramanga, forêt primaire humide et dégradée, alt. 800 m, 01/1970, *Onraedt 70M2030*, holotype BR.
- Lopholejeunea subfusca* (Nees) Schiffn. (Grolle, 1995; Pócs & Geissler, 2002; Zhu & Gradstein, 2005)
- Lopholejeunea tixieriana* Vanden Berghen (Grolle, 1995) **End**, Type – Antanidetra, 07/1977, *Tixier 10720*, holotype BR.
- Lopholejeunea utriculata* Steph. (Grolle, 1995) **End**, Type – unknown.
- Marchesinia excavata* (Mitt.) Schiffn. (Pócs & Geissler, 2002)
- Marchesinia madagassa* Steph. (Grolle, 1995)
- Mastigolejeunea auriculata* (Wilson) Schiffn. (Grolle, 1995)
- Mastigolejeunea rhodesica* (Vanden Berghen) E.W. Jones (Grolle, 1995)
- Metalejeunea cucullata* (Reinw. *et al.*) Grolle (Grolle, 1995)
- Microlejeunea africana* Steph. (Grolle, 1995)
- Microlejeunea fissistipula* Steph. (Grolle, 1995; Pócs & Geissler, 2002) **End**, Type – unknown.
- Microlejeunea inflata* Steph. (Grolle, 1995; Pócs & Geissler, 2002)
- Microlejeunea oblongistipula* (Gottsche) Pearson (Grolle, 1995)
- Microlejeunea papulosa* (Gottsche) Pearson (Grolle, 1995) **End**, Type – unknown.
- Odontolejeunea lunulata* (F. Weber) Schiffn. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
- Otolejeunea moniliata* Grolle (Grolle, 1985; Grolle, 1995) **End**, Type – Partie nord du massif du Morojeje, alt. 1450 m, *Guillaumet 4133/7*, holotype JE, isotypes PC, BR.
- Otolejeunea rabenorii* Tixier (Grolle, 1995) **End**, Type – Toamasina, route de Lakato, épiphyllie en forêt dense à graminées, 02/06/1979, *Tixier 12591*, holotype PC.
- Otolejeunea subana* Pócs (Pócs, 2004) **End**, Type – Toamasina Province, Mantadia Forest Reserve, North of Andasibe (Périnet), submontane rainforest, alt. 1030 m, S 18°52'20" E 48°28'26", 02/10/1994, *Pócs & Szabó 9485/R*, holotype EGR.
- Prionolejeunea grata* (Gottsche) Schiffn. (Grolle, 1995; Pócs & Geissler, 2002)
- Ptychanthus africanus* Steph. (Grolle, 1995; Ahonen *et al.*, 2005)
- Pycnolejeunea contigua* (Nees) Grolle (Grolle, 1995; He, 1999)
- Schiffneriolejeunea madagascariensis* (Steph.) Gradst. (Grolle, 1995) **End**, Type – unknown.
- Schiffneriolejeunea pappeana* (Nees) Gradst. (Grolle, 1995; Pócs & Geissler, 2002)

- Schiffneriolejeunea pappeana* var. *bidentata* Gradst. et Vanden Berghen (Grolle, 1995)
- Schiffneriolejeunea pappeana* var. *integra* Gradst. et Vanden Berghen (Grolle, 1995)
- Schiffneriolejeunea parviloba* (Steph.) Gradst. (Pócs & Geissler, 2002)
- Schiffneriolejeunea polycarpa* (Nees) Gradst. (Grolle, 1995; Pócs & Geissler, 2002)
- Symbiezidium barbiflorum* (Lindenb. et Gottsche) A. Evans (Sass-Gyarmati & Pócs, 2002)
- Symbiezidium madagascariense* Steph. (Gradstein & Van Beek, 1985; Grolle, 1995; Pócs, 1995)
- Taxilejeunea conformis* (Mont. et Nees) Steph. (Grolle, 1995; Pócs & Geissler, 2002)
- Taxilejeunea furcicornuta* Grolle (Grolle, 1995)
- Taxilejeunea sikorae* Steph. (Grolle, 1995) **End**, Type – unknown.
- Thysananthus spathulistipus* (Reinw. et al.) Lindenb. (Grolle, 1995; Pócs & Geissler, 2002) – Marojejy National Park, alt. 650 m, 24/11/2009, *Ah-Peng* 349, det. Ah-Peng, Bardat.
- Xylolejeunea grolleana* (Pócs) X.-L. He et Grolle (Pócs, 1999; He & Grolle, 2001)
- Lepidoziaceae**
- Amazoopsis diplopoda* (Pócs) J.J. Engel et G.L.S. Merr. (Grolle, 1995; Pócs, 1995)
- Bazzania curvidens* Steph. (Grolle, 1995) **End**, Type – Alakaty forest, 30/11/1889, Perrot, herb (N.S.).
- Bazzania deciduifolia* Onr. (Onraedt, 1977; Grolle, 1995) **End**, Type – Province de Fianarantsoa, forêt d'Ambatofitorahana, *Onraedt 71M5364*, holotype NAM, isotypes BR, JE.
- Bazzania decrescens* (Lehm. et Lindenb.) Trevis. (Grolle, 1995)
- Bazzania decrescens* subsp. *pumila* (Mitt.) Pócs (Pócs 1995)
- Bazzania decrescens* var. *ambahatrae* Pócs (Pócs & Geissler, 2002) **End**, Type – Manongarivo massif, alt. 1300-1400 m, *Pócs & Geissler PG 19742*, holotype EGR.
- Bazzania mascarena* (Steph.) Herzog (Grolle, 1995)
- Bazzania nitida* (F. Weber) Grolle (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
- Bazzania orbanii* Pócs (Pócs, 2010b) **End**, Type – SW Madagascar, Toliara Province, Isalo National Park, “Piscine naturelle”, a deep pool of a brook in a sandstone gorge, shaded by *Pandanus pulcher* trees, on soil, alt. 800 m, *Orbán 9455/J*, holotype EGR, isotypes MO, TAN.
- Bazzania perrotana* (Steph.) E.W. Jones (Jones, 1975; Grolle, 1995)
- Bazzania praerupta* (Reinw. et al.) Trevis. (Grolle, 1995; Pócs, 1995)
- Bazzania reflexa* (Gottsche) Steph. (Grolle, 1995) **End**, Type – unknown.
- Kurzia capillaries* (Sw.) Grolle subsp. *capillaris* (Pócs, 1995; Pócs & Geissler, 2002)
- Kurzia capillaris* (Renauld ex Steph.) Pócs subsp. *stephanii* (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
- Lepidozia africana* Steph. (Grolle, 1995)
- Lepidozia succida* Mitt. (Grolle, 1995; Pócs, 1995)
- Telaranea bischleriana* Pócs (Pócs, 2006)

Telaranea coactilis (Spruce) J.J. Engel *et* G.L.S. Merr. (Engel & Merrill, 2004)

Telaranea nematodes (Gottsche *ex* Austin) M. Howe (Grolle, 1995)

Lophocoleaceae

Chiloscyphus coadunatus (Sw.) J.J. Engel *et* R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)

Chiloscyphus concretus (Mont.) J.J. Engel *et* R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)

Chiloscyphus difformis (Nees) J.J. Engel *et* R.M. Schust. (Pócs & Geissler, 2002)

Chiloscyphus lucidus (Spreng. *ex* Lehm.) J.J. Engel *et* R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)

Chiloscyphus madagascariensis (Gottsche) J.J. Engel *et* R.M. Schust. (Grolle, 1995) End, Type – unknown.

Chiloscyphus martianus (Nees) J.J. Engel *et* R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)

Chiloscyphus muricatus (Lehm.) J.J. Engel *et* R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)

Chiloscyphus regularis Steph. (Grolle, 1995)

Clasmatocolea vermicularis (Lehm.) Grolle (Engel, 1980)

Conoscyphus trapezioides (Sande Lac.) Schiffn. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)

Heteroscyphus dubius (Gottsche) Schiffn. (Grolle, 1995)

Heteroscyphus splendens (Lehm. *et* Lindenb.) Grolle (Pócs, 1995; Pócs & Geissler, 2002)

Leptoscyphus expansus (Lehm.) Grolle (Grolle, 1995)

Leptoscyphus infuscatus (Mitt.) E.W. Jones (Pócs & Geissler, 2002)

Marchantiaceae

Marchantia debilis Goebel (Grolle, 1995)

Marchantia pappeana Lehm. subsp. *pappeana* (Grolle, 1995)

Mastigophoraceae

Mastigophora diclados (Brid. *ex* F. Weber) Nees (Grolle, 1995; Pócs & Geissler, 2002)

Metzgeriaceae

Metzgeria consanguinea Schiffn. (So, 2004)

Metzgeria furcata (L.) Dumort. (So, 2004)

Metzgeria leptoneura Spruce (Grolle, 1995; So, 2004)

Metzgeria madagassa Steph. (Grolle, 1995; So, 2004)

Metzgeria nudifrons Steph. (So, 2004)

Metzgeria quadrifaria Steph. (So, 2004)

Pallaviciniaceae

**Pallavicinia lyellii* (Hook.) – Ambavaniasy, réserve de Vohimana, forêt ombrophile d'altitude, jonction sol-racine au pied d'une micro falaise, alt. 870 m, S 18°55'19.5" E 48°30'05.7", 14/04/2010, Reeb, Andriamananatena & Bidault CRAE 40 & CRAE 48, TAN, det. Reeb & Andriamananatena; Ambavaniasy, réserve de Vohimana, bord de chemin vers relais du naturaliste, terre tassée, alt. 790 m, S 18°55'14.95" E 48°30'49.58", 16/04/2010 Reeb, Andriamananatena & Bidault CRAE 155, TAN, det. Reeb & Andriamananatena.

Symphogyna brasiliensis Nees *et* Mont. (Grolle, 1995)

**Symphogyna* aff. *podophylla* (Thunb.) Mont. *et* Nees. – Ambavaniasy, réserve de Vohimana, grande cascade microfalaise à 3 m du bord, face verticale, alt. 849 m, S 18°55'43.6" E 48°29'56.6", 15/04/2010, Reeb, Andriamanan-
atena & Bidault CRAE 87, TAN, det. Reeb & Andriamanan-
atena.

Symphogynopsis gottscheana (Mont. *et* Nees) Grolle (Grolle, 1995)

Plagiochilaceae

Plagiochila angusta Lindenb. (Grolle, 1995; Pócs & Geissler, 2002)

Plagiochila barteri Mitt. var. *barteri* (Grolle, 1995; Pócs & Geissler, 2002)

Plagiochila boivinii Steph. (Grolle, 1995)

Plagiochila boryana Gottsche *ex* Steph. (Grolle, 1995)

Plagiochila cambuena Steph. (Grolle, 1995)

Plagiochila drepanophylla Sande Lac. (Grolle, 1995)

Plagiochila fracta Pócs, *nom. inval.* (Pócs & Geissler, 2002; Heinrichs *et al* 2005)

Plagiochila granditexta Steph. (Grolle, 1995) **End**, Type – *Hildebrandt*, herb (N.S.).

Plagiochila incerta Gottsche (Grolle, 1995; Pócs & Geissler, 2002)

Plagiochila integerrima Steph. (Grolle, 1995)

Plagiochila kiaeri Gottsche (Grolle, 1995; Pócs & Geissler, 2002)

Plagiochila paucidentata Mont. *et* Gottsche (Grolle, 1995; Pócs & Geissler, 2002)

Plagiochila pectinata Willd. *ex* Lindenb. (Grolle, 1995; Pócs & Geissler, 2002)

Plagiochila punctata (Taylor) Taylor (Grolle, 1995; Pócs & Geissler, 2002; Heinrichs *et al.*, 2005)

Plagiochila repanda (Schwaegr.) Lindenb. (Grolle, 1995)

Plagiochila repanda var. *perrotana* (Steph.) Vanden Berghen (Grolle, 1995)

Plagiochila rodriguezii Steph. (Grolle, 1995)

Plagiochila squamulosa var. *crispulo-caudata* (Gottsche) Vanden Berghen (Grolle, 1995)

Plagiochila squamulosa var. *sinuosa* (Mitt.) Vanden Berghen (Grolle, 1995)

Plagiochila stricta Lindenb. (Lindner *et al.*, 2004)

Plagiochila terebrans Nees *et* Mont. *ex* Lindenb. (Grolle, 1995; Pócs & Geissler, 2002)

Pleuroziaceae

Pleurozia gigantea (F. Weber) Lindb. (Pócs & Geissler, 2002)

Porellaceae

Porella abyssinica var. *hoehnelii* (Steph.) Pócs (Grolle, 1995)

Porella cucullistipula Steph. (Grolle, 1995)

Porella madagascariensis (Nees *et* Mont.) Trevis. (Grolle, 1995)

Porella montantii (Steph.) E.W. Jones (Grolle, 1995)

Porella triquetra (Steph.) E.W. Jones (Grolle, 1995)

Radulaceae

Radula ankefinensis Gottsche *ex* Steph. (Grolle, 1995; Grolle, 2001; Pócs & Geissler, 2002)

Radula appressa Mitt. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)

Radula boryana (F. Weber) Mont. (Grolle, 1995; Grolle, 2001; Pócs & Geissler, 2002)

Radula comorensis Steph. (Pócs & Geissler, 2002)

- Radula fulvifolia* (Hook.f. *et* Taylor) Gottsche *et al.* (Grolle, 2001)
Radula madagascariensis Gottsche (Yamada, 1975; Grolle, 1995; Pócs, 1995; Grolle, 2001)
Radula marojezica E.W. Jones (Grolle, 1995) **End**, Type – Province Antsiranana, Parc National de Marojejy, Pócs 90114/BN, holotype E, isotype and paratype EGR.
Radula quadrata Gottsche (Grolle, 1995)
Radula silvestris Gottsche (Grolle, 1995)
Radula stenocalyx Mont. (Grolle, 1995; Pócs, 1995; Grolle, 2001; Pócs & Geissler, 2002)
Radula voluta Taylor *ex* Gottsche *et al.* (Grolle, 1995; Pócs, 1995; Grolle, 2001; Pócs & Geissler, 2002)

Ricciaceae

- Riccia atromarginata* var. *jovent-astiae* Rauh & Buchloh (Grolle, 1995)
Riccia cavernosa Hoffm. (Grolle, 1995)
Riccia crinita Taylor (Grolle, 1995)
Riccia perssonii Sultan Khan (Perold, 1995)
 **Riccia purpurascens* Lehm. – Makirovana, Talus vertical en bord de rizière, Ambodimanga au pied de Makirovana, alt. 41 m, S 14°11'13.6" E 49°59'09.2", 03/05/2010, Reeb CR 203, det. Reeb & Bardat.

Scapaniaceae

- Anastrophyllum piligerum* (Nees) Steph. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
Andrewsianthus aberrans (Nees *et* Mont.) Grolle (Pócs, 1995)
Plicanthus birmensis (Steph.) R.M. Schust. (Grolle, 1995)
Plicanthus hirtellus (F. Weber) R.M. Schust. (Grolle, 1995; Pócs & Geissler, 2002)

Schistochilaceae

- Gottschea neesii* (Mont.) R.M. Schust. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
Schistochila alata (Lehm.) Schiffn. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002)
Schistochila piligera Steph. (Grolle, 1995; Pócs, 1995; Pócs & Geissler, 2002) **End**, Type – Camboué, herb (N.S.).

Targioniaceae

- Targionia hypophylla* L. (Grolle, 1995)
 **Targionia dioica* Schiffn. – Biosphere Reserve and National Park, Mananara-Nord, Toamasina, alt. 220 m, 17/08/1998, Pócs & Szabó 9878/CY, EGR.

Hornworts reported from Madagascar

Anthocerotaceae

- Anthoceros* sp. (Grolle, 1995)
 **Dendroceros* cf. *africanus* Steph. – Réserve Spéciale Angavokely, alt. 1750 m, 11/2009, Bardat JB MAD 147, det. Bardat.

Notothyladaceae

- Phaeoceros carolinianus* (Michx.) Prosk. (Grolle, 1995)

Mosses reported from Madagascar

Amblystegiaceae

Amblystegium chalaropelma Müll.Hal. ex Renauld (Crosby *et al.*, 1983) **End**,
Type – Zone du plateau central, Imerina Oriental, *Hildebrandt 2076*,
herb. (N.S.).

Amblystegium riparium (Hedw.) Bruch, Schimp. *et* W.Guembel (Crosby *et al.*,
1983)

Hygrohypnum causequei (Renauld & Cardot) Cardot (Crosby *et al.*, 1983) **End**,
Type – Entre Tananarive et Betafo, 1894, *Caussèque*, holotype PC.

Andreaeaceae

Andreaea subulata Harv. (Crosby *et al.*, 1983)

Andreaea tsaratananae Thér. (Crosby *et al.*, 1983)

Anomodontaceae

Herpetineuron toccoae (Sull. *et* Lesq.) Cardot (Touw, 1993)

Archidiaceae

**Archidium ohioense* Schimp. ex Müll.Hal. – Beza mahafaly, Betioky, Riverine
forest adjacent to Sakamena river, open ground on forest floor, alt. 130 m,
S 23°39' E 44°38', 18/05/1987, *Phillipson 1818*, TAN.

**Archidium subulatum* Müll.Hal. – Beloha Tsihombe, dalle de gneiss, 10/04/1971,
Cornet & Cremers 2014, TAN.

Bartramiaceae

Bartramia gigantea Bory (Crosby *et al.*, 1983)

Bartramia longifolia Hook. (Crosby *et al.*, 1983)

Breutelia diffracta Mitt. (Crosby *et al.*, 1983)

Breutelia gnaphalea P. Beauv. (Crosby *et al.*, 1983)

Breutelia madagassa Thér. var. *madagassa* (Crosby *et al.*, 1983) **End**, Type –
Mont Tsaratanana, alt. 1200 m, 04/1924, *Perrier de la Bathie*, holotype PC.

Breutelia microdonta (Mitt.) Broth. (Crosby *et al.*, 1983; Virtanen, 1997)

Breutelia perrieri Thér. (Crosby *et al.*, 1983)

Breutelia sciuroides Thér. (Crosby *et al.*, 1983)

Breutelia stuhlmannii Broth. (De Sloover, 1975; Crosby *et al.*, 1983)

Breutelia viguieri Cardot (Crosby *et al.*, 1983) **End**, Type – Ambatolampy,
ruisselet près du sommet du Tsiarafajavona, alt. 2575 m, 28/11/1912, *Viguier*
1688ter, holotype PC.

Philonotis byssiformis Müll.Hal. (Crosby *et al.*, 1983) **End**, Type – Zone inférieure
des forêts, Nosy Be, *Hildebrandt*, holotype PC.

Philonotis hastata (Duby) Wijk *et* Margad. (Crosby *et al.*, 1983)

Philonotis mauritiana Aongstr. (Crosby *et al.*, 1983)

Philonotis mauritiana var. *stricta* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**,
Type – Plateau central, environs de Tananarive, *Camboué*; Entre
Tananarive et Betafo, *Caussèque*. Fianarantsoa, *Besson*; Ambositra,
Soula; Mont Ambohijanahary, PC, holotype (N.S.).

Philonotis perpusilla Cardot (Crosby *et al.*, 1983) **End**, Type – Zone de savane
occidentale, Marovoay, *Mathieu*, herb (N.S.).

Philonotis perrieri Thér. (Crosby *et al.*, 1983)

Philonotis sparsifolia (Hampe) A. Jaeger (Crosby *et al.*, 1983)

Brachytheciaceae

- Aerolindigia capillacea* (Hornsch.) M. Menzel (Crosby *et al.*, 1983)
Brachythecium borgenii (Hampe) A. Jaeger (Crosby *et al.*, 1983)
Brachythecium decurrens Cardot (Crosby *et al.*, 1983)
Eurhynchium spinulinerve Kiaer ex Cardot (Crosby *et al.*, 1983)
Eurhynchium striatum (Schreb. ex Hedw.) Schimp. (Crosby *et al.*, 1983)
Helicodontium fabroniopsis Müll. Hal. (Crosby *et al.*, 1983) **End**, Type – Zone supérieure des forêts, troncs d'arbres à Andrangoloaka, *Sikora*, herb (N.S.).
Palamocladium leskeoides (Hook.) E. Britton (Crosby *et al.*, 1983; Hofmann, 1997)
Rhynchostegiella microtheca (Renauld et Cardot) Broth. (Crosby *et al.*, 1983)
Rhynchostegium angustifolium Renauld & Cardot (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, forêt d'Analamazaotra, *Camboué & Campenon*, herb (N.S.).
Rhynchostegium comorae (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983)
Rhynchostegium distans Besch. (Crosby *et al.*, 1983)
Rhynchostegium nervosum (Renauld) Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, monts Ankaratra, *Borgen 61*, lectotype BM, isolectotype THR.
Rhynchostegium pseudodistans Cardot (Crosby *et al.*, 1983)
Schimperella rhynchostegioides Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, alt. 1200 m, 04/1924, *Perrier de la Bathie 176 p.p.*, lectotype PC.
Squamidium brasiliense (Hornsch.) Broth. (Crosby *et al.*, 1983; Allen & Crosby, 1986; Delgadillo, 1995)

Bruchiaceae

- Trematodon curvicollis* Cardot (Crosby *et al.*, 1983) **End**, Type – Entre Savondronina et Ranomafana, *Besson*, holotype PC.
Trematodon decaryi Thér. (Crosby *et al.*, 1983) **End**, Type – Vallée de l'Anony, sur talus humide, 05/08/1921, *Decary*, holotype PC.
Trematodon lacunosus Renauld & Cardot (Crosby *et al.*, 1983) **End**, Type – Entre Savondronina et Ranomafana, 1892, *Besson*, PC.
Trematodon longicollis Michx. (Crosby *et al.*, 1983)
Trematodon platybasis Müll.Hal. (Crosby *et al.*, 1983) **End**, Type – Alasora, Ambohipo, Tananarive, alt. 1250 m, *Camboué*, holotype PC.
Trematodon reticulatus Müll.Hal. ex Geh. (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, à l'Est d'Ambatondrazaka, *Rutemberg*, herb (N.S.).
Trematodon viguieri Cardot (Crosby *et al.*, 1983)

Bryaceae

- Anomobryum filiforme* var. *madagassum* Renauld et Cardot (Crosby *et al.*, 1983) **End**, Type – Zone de plateau central, Imerina, *Camboué*, herb (N.S.).
Anomobryum julaceum (P. Gaertn., B. Mey. et Scherb.) Schimp. var. *julaceum* (Ochi, 1972; Crosby *et al.*, 1983)
Brachymenium acuminatum Harv. (Ochi, 1972; Crosby *et al.*, 1983; Delgadillo, 1995)
Brachymenium apiculatum P. Beauv. (Crosby *et al.*, 1983)
Brachymenium capitulatum (Mitt.) Kindb. (Crosby *et al.*, 1983)

- Brachymenium exile* (Dozy et Molk.) Bosch et Sande Lac. (Ochi, 1972; Crosby et al., 1983; Delgadillo, 1995)
- Brachymenium leptophyllum* (Bruch et Schimp. ex Müll.Hal.) Bruch & Schimp. ex A. Jaeger (Crosby et al., 1983)
- Brachymenium madagassum* Hampe (Ochi, 1972; Crosby et al., 1983) **End**, Type – Plateau central, 1869, *Borgen*, holotype PC.
- Brachymenium nepalense* Hook. (Ochi, 1972; Crosby et al., 1983; Pócs & Geissler, 2002)
- Brachymenium nigrescens* Besch. (Ochi, 1972; Crosby et al., 1983)
- Brachymenium notarisii* (Mitt.) A.J. Shaw (Crosby et al., 1983)
- Brachymenium philonotula* Broth. (Ochi, 1972; Crosby et al., 1983)
- Brachymenium pulchrum* Hook. (Ochi, 1972; Crosby et al., 1983; Tixier, 1995)
- Brachymenium rigidum* Broth. et Paris (Crosby et al., 1983)
- Bryum albo-marginatum* Cardot (Ochi, 1972; Crosby et al., 1983) **End**, Type – Mont Tsaratanana, alt. 1200-2400 m, 4/1924, *Perrier de la Bathie s. n.*, holotype PC#
- Bryum alpinulum* var. *levieri* Renaud et Cardot (Crosby et al., 1983) **End**, Type – Zone inférieure des forêts, forêt de Fito, *Perrot*, holotype FI#
- Bryum alpinum* Huds. ex With. var. *alpinum* (Ochi, 1972; Ochi, 1973; Crosby et al., 1983)
- Bryum apiculatum* Schwaegr. (Ochi, 1972; Crosby et al., 1983)
- Bryum arachnoideum* Müll.Hal. (Ochi, 1972; Crosby et al., 1983)
- Bryum argenteum* Hedw. var. *argenteum* (Ochi, 1972; Crosby et al., 1983; Pócs & Geissler, 2002)
- Bryum aubertii* (Schwaegr.) Brid. (Ochi, 1972; Crosby et al., 1983)
- Bryum billardierei* Schwaegr. var. *billardierei* (Ochi, 1972; Mohamed, 1979; Crosby et al., 1983)
- Bryum caespiticium* Hedw. var. *caespiticium* (Pócs & Geissler, 2002)
- Bryum capillare* Hedw. var. *capillare* (Ochi, 1972; Crosby et al., 1983)
- Bryum coronatum* Schwaegr. (Ochi, 1972; Crosby et al., 1983; Pócs & Geissler, 2002)
- Bryum dichotomum* Hedw. (Crosby et al., 1983)
- Bryum erythrocaulon* (Schwäegr.) Brid. (Mohamed, 1979; Crosby et al., 1983)
- Bryum huillense* Welw. et Duby (Ochi, 1972; Crosby et al., 1983; Pócs & Geissler, 2002)
- Bryum imerinanus* O'Shea (O'Shea, 2008)
- Bryum leptospeiron* Müll.Hal. (Crosby et al., 1983)
- Bryum megalacrion* Schwaegr. (Ochi, 1972; Crosby et al., 1983)
- Bryum neelgheriense* var. *wichurae* (Broth.) Mohamed (Pócs & Geissler, 2002)
- Bryum paradoxum* Schwaegr. (Ochi, 1972; Crosby et al., 1983; Delgadillo, 1995)
- Bryum perrieri* Thér. (Crosby et al., 1983) **End**, Type – Forêt du centre, alt. 2000 m, *Perrier de la Bathie 12127p.p.*, holotype PC.
- Bryum pseudotriquetrum* (Hedw.) P. Gaertn., B. Mey. et Scherb. var. *pseudotriquetrum* (Crosby et al., 1983)
- Bryum purpureonigrum* Duby (Crosby et al., 1983) **End**, Type – unknown.
- Bryum savondronicus* O'Shea (Crosby et al., 1983; O'Shea, 2008) **End**, Type – Between Savondronina and Ranomafana, *Besson*, herb (N.S.).
- Bryum subargenteum* Hampe (Ochi, 1972; Crosby et al., 1983)
- Bryum viguieri* Thér. (Ochi, 1972; Crosby et al., 1983)

- Bryum voeltzkowii* Broth. (Ochi, 1972; Mohamed, 1979; Crosby *et al.*, 1983)
Mniobryum perlaxum Thér. et P. de la Varde (Crosby *et al.*, 1983) **End**, Type – Totohaza, 05/1931, Grainville, holotype PC.
Rhodobryum commersonii (Schwaegr.) Brid. (Crosby *et al.*, 1983; Pócs & Geissler, 2002)
Rhodobryum giganteum (Schwaegr.) Paris (Crosby *et al.*, 1983; Ochi, 1972)
Rhodobryum ontariense (Kindb.) Paris (Crosby *et al.*, 1983)
- Calymperaceae**
Calymperes afzelii Sw. (Crosby *et al.*, 1983; Pócs & Geissler, 2002)
Calymperes erosum Müll.Hal. (Crosby *et al.*, 1983)
Calymperes hispidum Renaud et Cardot (Crosby *et al.*, 1983; Ellis, 1988)
Calymperes loucoubense Besch. (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Nosy Be, Lokobe, 1879, Marie, holotype BM.
Calymperes palisotii Schwaegr. (Crosby *et al.*, 1983)
Calymperes pallidum Mitt. (Crosby *et al.*, 1983; Delgadillo, 1995)
**Calymperes sanctae-mariae* var. *mayottense* Besch. – Mananjary, tronc de *Pandanus*, 14/07/1972, Cornet & Cremers 2250, TAN.
Calymperes taitense (Sull.) Mitt. (Crosby *et al.*, 1983; Orbán, 1995)
Calymperes tenerum Müll.Hal. (Crosby *et al.*, 1983)
Calymperes venezuelanum (Mitt.) Broth. ex Pittier (Orbán, 2000)
Leucophanes hildebrandtii Müll.Hal. (Crosby *et al.*, 1983; Salazar Allen, 1993)
Leucophanes renauldii Cardot (Crosby *et al.*, 1983; Salazar Allen, 1993; Pócs & Geissler, 2002)
Leucophanes rodriguezii Müll.Hal. (Salazar Allen, 1993)
Mitthyridium fasciculatum (Hook. et Grev.) H. Rob. var. *fasciculatum* (Reese, 1991)
Mitthyridium subflavum (Renaud & Cardot) H. Rob. (Müller, 1897; Crosby *et al.*, 1983)
Octoblepharum africanum (Broth.) Cardot (Crosby *et al.*, 1983)
Octoblepharum albidum Hedw. (Crosby *et al.*, 1983; Pócs & Geissler, 2002)
Syrrhopodon africanus (Mitt.) Paris var. *africanus* (Crosby *et al.*, 1983)
Syrrhopodon africanus var. *mandrakensis* (Tixier) W.D. Reese (Tixier, 1992; Pócs & Geissler, 2002)
Syrrhopodon albidus (E.B. Bartram) L.T. Ellis subsp. *integrifolius* (Pócs & Geissler, 2002)
Syrrhopodon apertifolius Besch. (Ellis, 1995)
Syrrhopodon armatissimus W.D. Reese (Reese, 1991; Orbán, 1995)
Syrrhopodon armatus (Bizot et Onr.) Orbán and W.D. Reese subsp. *insularis* (Orbán, 1977)
Syrrhopodon asper Mitt. (Een, 1993)
Syrrhopodon cuneifolius Thér. (Orbán, 1981; Crosby *et al.*, 1983; Pócs & Geissler, 2002) **End**, Type – Massif de l'Ankaizina, alt. 1200 m, 04/1923, Decary, holotype PC.
Syrrhopodon dimorphophyllus L.T. Ellis (Ellis, 2005)
Syrrhopodon gardneri (Hook.) Schwaegr. (Orbán, 1981; Crosby *et al.*, 1983; Ellis, 2002; Pócs & Geissler, 2002)
Syrrhopodon gaudichaudii Mont. (Orbán, 1981; Crosby *et al.*, 1983; Ellis, 2005)
Syrrhopodon graminifolius Renaud et Cardot (Orbán, 1981; Crosby *et al.*, 1983)

Syrrhopodon hispidocostatus Renaud *et* Cardot *in* Renaud (Orbán, 1978; Orbán, 1981; Crosby *et al.*, 1983; Pócs & Geissler, 2002; Ellis, 2003; Ellis, 2005)

Syrrhopodon involutus Schwaegr. (Orbán, 1981; Crosby *et al.*, 1983)

Syrrhopodon mauritanus Müll.Hal. *ex* Aongstr. (Orbán, 1981; Crosby *et al.*, 1983)

Syrrhopodon parasiticus (Sw. *ex* Brid.) Besch. (Crosby *et al.*, 1983)

Syrrhopodon pottioides Orbán (Orbán, 1995)

Syrrhopodon prolifer var. *acanthoneuros* (Müll.Hal.) Müll.Hal. (Orbán, 1981; Crosby *et al.*, 1983; Ellis, 2003)

Syrrhopodon prolifer Schwaegr. var. *prolifer* (Orbán, 1981; Crosby *et al.*, 1983; Delgadillo, 1995)

Syrrhopodon pulcher W.D. Reese (Orbán, 1995)

Syrrhopodon spiralis Renaud *et* Cardot (Ellis, 2005)

Syrrhopodon tixieri W.D. Reese (Tixier, 1992) **End**, Type – Ranomafana, Fianarantsoa, route de Mananjary, pk 24, corticole, alt. 900 m, *Tixier 10152*, holotype PC, paratype MO.

Syrrhopodon vardei L.T. Ellis (Ellis, 2005)

Catagoniaceae

Catagonium nitens (Brid.) Cardot subsp. *nitens* (Crosby *et al.*, 1983)

Cryphaeaceae

Cryphaea jamesonii Taylor (Crosby *et al.*, 1983; Rao, 2001)

Cryphaea rutenbergii Müll.Hal. (Crosby *et al.*, 1983; Rao, 2001)

Schoenobryum concavifolium (Griff.) Manuel (Crosby *et al.*, 1983; O'Shea, 2003)

Daltoniaceae

Adelothecium bogotense Hampe (Crosby *et al.*, 1983; Delgadillo, 1995)

Calypstrochaeta asplenioides (Brid.) Crosby (Crosby *et al.*, 1983)

Daltonia angustifolia Dozy *et* Molk. var. *angustifolia* (Crosby *et al.*, 1983)

Daltonia cardotii Bizot *et* Onr. (Crosby *et al.*, 1983)

Daltonia forsythii Cardot (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, forêt d'Ambohimombo, alt. 1350 m, 1895, *Forsyth Major*, holotype PC.

Daltonia latimarginata Besch. (Crosby *et al.*, 1983)

Daltonia latimarginata var. *madagassa* Renaud (Crosby *et al.*, 1983)

**Distichophyllum mascarenicum* Besch. – Marojeje National Park, scattered elfin forest, soil bank above the stream, S 14°26' E 49°45', alt. 1050 m, *Magill, Pócs & La Farge 9971*, TAN.

Distichophyllum rakotomariae Crosby (Crosby *et al.*, 1983; Touw, 1993) **End**, Type – Montagne d'Ambre, Diégo-Suarez, alt. 900-1100 m, *M.R. & C.A Crosby 6883*, holotype MO, isotypes PC, TAN.

Dicranaceae

Anisothecium madagassum Thér. (Crosby *et al.*, 1983) **End**, Type – Montagne d'Ambre, forêt, alt. 1000-1200 m, 10/1926, *Perrier de La Bathie*, holotype PC.

Aongstroemia filiformis (P. Beauv.) Wijk *et* Margad. (Crosby *et al.*, 1983; Delgadillo, 1995)

Aongstroemia julacea (Hook.) Mitt. (Crosby *et al.*, 1983)

Dicranella acroclada Cardot (Crosby *et al.*, 1983)

- Dicranella borbonica* var. *madagascariensis* Thér. (Crosby *et al.*, 1983) **End**, Type – Montagne d'Ambre, Forêt du versant oriental, 1899, Girod, holotype PC.
- Dicranella madagassa* Renaud (Crosby *et al.*, 1983)
- Dicranella pervilleana* Besch. (Crosby *et al.*, 1983)
- Dicranella polii* Renaud *et* Cardot (Crosby *et al.*, 1983)
- Dicranella subsubulata* (Hampe *ex* Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983)
- Dicranoloma billardieri* (Brid. *ex* Anon.) Paris (Crosby *et al.*, 1983)
- Dicranoloma billardieri* var. *patentifolium* (Renaud *et* Paris) Thér. (Crosby *et al.*, 1983)
- Dicranoloma billardieri* var. *scopareolum* (Müll.Hal.) Thér. (Crosby *et al.*, 1983)
- Dicranum johnstonii* Mitt. (Pócs & Geissler, 2002)
- Holomitrium borbonicum* Besch. (Crosby *et al.*, 1983)
- Holomitrium borbonicum* var. *hamatum* (Müll.Hal.) Thér. (Crosby *et al.*, 1983)
- Holomitrium camptocarpum* P. de la Varde (Crosby *et al.*, 1983) **End**, Type – Pentes orientales du massif de Marojejy, à l'Ouest de la rivière Manantenina, affluent de la Lokoho, sylvie à lichens sur gneiss et quartzite, alt. 1400 m, 15/12/1948, *Humbert*, holotype PC.
- Holomitrium cylindraceum* var. *cucullatum* (Besch.) Wijk *et* Margad. (Crosby *et al.*, 1983)
- Holomitrium cylindraceum* (P. Beauv.) Wijk & Margad. var. *cylindraceum* (Crosby *et al.*, 1983)
- Holomitrium cylindraceum* var. *obtusifolium* (Besch.) Wijk *et* Margad. (Crosby *et al.*, 1983)
- Holomitrium gracilisetum* Thér. (Crosby *et al.*, 1983) **End**, Type – Ankaizina, alt. 1200-1500 m, 04/1933, *Decary*, holotype PC.
- Holomitrium hillieri* Thér. (Crosby *et al.*, 1983) **End**, Type – Forêt de Manongarivo, entre Nosy Be et Analalava, alt. 600 m, S 13°55'00" E 48°24'00", 1909, *Perrier de la Bathie*, holotype PC.
- Holomitrium lepervanchei* Thér. (Crosby *et al.*, 1983)
- Holomitrium rhyparodictyon* P. de la Varde (Crosby *et al.*, 1983) **End**, Type – Pente orientale du massif de Marojejy, sylvie à lichens et végétation éricoïde des sommets, affluent de la Lokoho, alt. 1500 m, 17/12/1948, *Humbert*, holotype PC.
- Holomitrium subglobosum* Thér. (Crosby *et al.*, 1983) **End**, Type – Ifanadina, forêt, herb (N.S.).
- Leptotrichella minuta* (Hampe) Ochyra (Crosby *et al.*, 1983)
- Leptotrichella pallidiseta* (Brid.) Ochyra (Crosby *et al.*, 1983) **End**, Type – unknown.
- Leucoloma albocinctum* Renaud *et* Cardot (Crosby *et al.*, 1983; La Farge, 2002c)
- Leucoloma allorgei* Thér. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Befotaka, 20/08/1926, *Decary*, holotype PC.
- Leucoloma ambreanum* Renaud *et* Cardot (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Montagne d'Ambre, près de Diégo-Suarez, 1890, *Chénagon*, holotype PC.
- Leucoloma bifidum* (Brid.) Brid. (Crosby *et al.*, 1983)
- Leucoloma boivinianum* Besch. var. *boivinianum* (Crosby *et al.*, 1983)

- Leucoloma boivinianum* var. *brevifolium* Renaud (Crosby *et al.*, 1983) **End**, Type – Betsileo, entre Savondronina et Ranomafana, 1892, *Besson*, holotype PC.
- Leucoloma brevioperculatum* Dixon (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Vohémar, 1814, *Thompson 30*, holotype BM.
- Leucoloma brotheri* Renaud (Crosby *et al.*, 1983; La Farge, 2002c)
- **Leucoloma caespitulans* (Müll.Hal.) A. Jaeger – Montagne des Français, bois mort, alt. 400 m, 25/08/1973, *Cremers 2657*, TAN.
- Leucoloma candidum* Broth. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Sainte Marie, East Madagascar, 1904, *Voeltzkow*, holotype BR.
- Leucoloma capillifolium* Renaud (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Sainte Marie, Sahasifotro, troncs d'arbres, 1894, *Darbould*, lectotype PC.
- Leucoloma chrysobasilare* (Müll.Hal.) A. Jaeger var. *chrysobasilare* (Crosby *et al.*, 1983)
- Leucoloma cirrosulum* Renaud (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Forêt d'Analamazaotra, 1891, *Camboué & Campenon*, holotype PC.
- Leucoloma crosbyi* La Farge-England (La Farge-England, 1992; La Farge, 2002a; La Farge, 2002c) **End**, Type – Diégo-Suarez, Montagne d'Ambre, Parc National, 10 km along trail between Petit Lac and Grand Lac, S 12°34' E 49°12', 1972, *M.R. & C.A Crosby 7167, 13.xi.* holotype MO, isotypes ALTA, TAN.
- Leucoloma cuneifolium* (Hampe ex Müll.Hal. et Geh.) C.H. Wright (Crosby *et al.*, 1983; La Farge, 2002b; La Farge, 2002c)
- Leucoloma decaryi* Thér. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Massif d'Ankaizinana, 10/06/1923, *Decary*, holotype PC.
- Leucoloma delicatulum* Renaud (Crosby *et al.*, 1983; La Farge, 2002c)
- Leucoloma dichelymoides* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983; La Farge, 2002a)
- Leucoloma fontinaloides* Dixon (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c) **End**, Type – Ambohimomba forest, Tanala, 05/01/1895, *Forsyth-Major 473 b*, holotype BM.
- Leucoloma fuscifolium* Besch. (Crosby *et al.*, 1983)
- Leucoloma fuscifolium* var. *crispatum* Renaud (Crosby *et al.*, 1983)
- Leucoloma garnieri* Paris & Renaud (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Ad radices arboris “Jisy”, Dictae secus rivulum “Pleurs des Bœufs”, 24/08/1904, *Savelli*, lectotype PC.
- Leucoloma garnieri* f. *aquaticum* Thér. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Massif de l'Andringitra, 1921, *Perrier de la Bathie*, holotype PC.
- Leucoloma grandidieri* Renaud et Cardot (Crosby *et al.*, 1983; La Farge-England, 1992; La Farge, 2002a; La Farge, 2002c) **End**, Type – Forêt d'Analamazaotra, 1891, *Camboué & Campenon*, lectotype PC.
- Leucoloma grimmiioides* P. de la Varde (Crosby *et al.*, 1983; La Farge, 2002b; La Farge, 2002c)
- Leucoloma humbertii* P. de la Varde (Crosby *et al.*, 1983; La Farge, 2002b; La Farge, 2002c) **End**, Type – Pentès orientales du massif de Marojejy, à l'ouest de la rivière Manantenina, affluent de la Lokoho sylvie à lichens sur gneiss et quartzite, alt. 1400 m, 15/12/1948, *Humbert*, holotype PC.
- Leucoloma incrassatum* Thér. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Massif de l'Ikongo, rochers humides en forêt, *Decary*, holotype PC.

- Leucoloma lepervancheri* Besch. (La Farge, 2002a; La Farge, 2002c)
- Leucoloma longifolium* (Brid.) Wijk *et* Margad. (Crosby *et al.*, 1983; La Farge, 2002c)
- Leucoloma madagascariense* La Farge (La Farge, 2002a; La Farge, 2002c) **End**, Type – Province Tamatave, Andasibe (Périnet), Reserve Forestière, montane rainforest with shady, wet habitats along stream leading to lac vert, Canopy reaching 25 m, mostly closed, with tall palms and bamboo, alt. 920-980 m, S 18°54'00" E 48°25'3", 16/03/1990, *La Farge-England 5788*, holotype ALTA, isotypes MO,TAN.
- Leucoloma marojeziense* La Farge (La Farge, 2002a; La Farge, 2002b; La Farge, 2002c) **End**, Type – Province Diégo-Suarez, Tahirin-javaboahary Marojejy, north of Manantenina and Loko River Valley, slopes of the Marojejy massif above Mandena village, S 14°26' E 49°44', *La Farge-England 6298*, holotype ALTA, isotypes MO, TAN.
- Leucoloma membranaceum* La Farge (La Farge, 2002a)
- Leucoloma ochrobasilare* Ren. (Crosby *et al.*, 1983; La Farge, 2002c)
- Leucoloma ochrobasilare* (Thér.) La Farge subsp. *longifolium* (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c) **End**, Type – Mont Tsaratanana, forêt à sous bois herbacé, alt. 1200-2400 m, 04/1924, *Perrier de la Bathie*, holotype PC.
- Leucoloma ochrobasilare* Renauld subsp. *ochrobasilare* (Crosby *et al.*, 1983; La Farge, 2002a)
- Leucoloma oncophorellum* Müll.Hal. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – lectotype PC.
- Leucoloma perrieri* Thér. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Forêt à l'Est de Tananarive, 11/1927, *Perrier de la Bathie*, holotype PC, isotype FH.
- Leucoloma persecundum* Besch. (Crosby *et al.*, 1983)
- Leucoloma persecundum* var. *perrotii* Renauld (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Environs d'Andevoranto, 1895, *Perrot*, lectotype BM.
- Leucoloma pumilum* C.H. Wright (Crosby *et al.*, 1983) **End**, Type – Sur le Plateau central, à Alaby, près de Maritandrano, *Rutenberg*, herb (N.S.).
- Leucoloma pusillum* Cardot (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Diégo-Suarez, zone inférieure des forêts, sur écorces, *Chénagon*, lectotype PC.
- Leucoloma rutenbergii* (Geh.) C.H. Wright (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Ambatondrazaka, Analamazaotra, *Rutenberg*, lectotype PC.
- Leucoloma rutenbergii* var. *abbreviatum* Renauld (Crosby *et al.*, 1983) **End**, Type – Forêt d'Alakaty, *Perrot*; Forêt d'Analamazaotra, *Camboué & Campenon*; holotype (N.S.).
- Leucoloma rutenbergii* var. *elatum* Renauld (Crosby *et al.*, 1983; La Farge, 2002c)
- Leucoloma rutenbergii* var. *perrotii* Renauld (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Environs d'Andevoranto, 1895, *Perrot*, holotype PC, isotypes BR, FH.
- Leucoloma sanctae-mariae* Besch. (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c)
- Leucoloma seychellense* Besch. (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c)
- Leucoloma sinuosulum* Müll.Hal. *ex* Besch. (Crosby *et al.*, 1983)

- Leucoloma squarrosulum* (Geh.) Wright (Crosby *et al.*, 1983) **End**, Type – Forêt de Vondrozona, 11/1877, *Rutenberg*, holotype PC.
- Leucoloma subchrysobasilare* Renauld (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c) **End**, Type – In montibus Ankaratra, 1877, *Borgen*, lectotype PC.
- Leucoloma talazaccii* Renauld *et* Cardot (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c) **End**, Type – Ambondrombe, 1894, *Talazac*, holotype PC, isotypes BR, PC, S.
- Leucoloma thraustum* Hampe *ex* Besch. (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c) **End**, Type – Alamazantraskoven, *Borchgrevink*, lectotype BM.
- Leucoloma thuretii* Besch. (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c) **End**, Type – Côte Est, près de la cascade de Simiang, *Bernier*, lectotype BM.
- Leucoloma tuberosum* Renauld (Crosby *et al.*, 1983; La Farge, 2002a; La Farge, 2002c) **End**, Type – Forêt d'Analamazaotra, 1891, *Camboué & Campenon*, holotype PC.
- Leucoloma villaumei* Thér. (Crosby *et al.*, 1983; La Farge, 2002c) **End**, Type – Betsileo, *Villaume*, holotype PC.
- Microcampylopus laevigatus* (Thér.) Giese & J.-P. Frahm (Crosby *et al.*, 1983; Giese & Frahm, 1985)
- Pseudophemerum nitidum* (Hedw.) Reimers (Crosby *et al.*, 1983)
- Ditrichaceae**
- Ceratodon purpureus* (Reichardt) Burley subsp. *convolutus* (Crosby *et al.*, 1983; Burley & Pritchard, 1990; Een, 1993)
- Distichum capillaceum* (Hedw.) Bruch, Schimp. *et* W. Guembel var. *capillaceum* (Crosby *et al.*, 1983)
- Ditrichum difficile* (Duby) M. Fleisch. (Crosby *et al.*, 1983; Delgadillo, 1995)
- Ditrichum luteum* Dixon *et* Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, *Perrier de la Bathie*, holotype PC.
- Ditrichum madagassum* (Renauld *et* Cardot) Paris (Crosby *et al.*, 1983) **End**, Type – Andrangoloaka, 1891, *Sikora*, holotype PC.
- Ditrichum pallidum* (Hedw.) Hampe (Crosby *et al.*, 1983)
- Garckea flexuosa* (Griff.) Margad. *et* Nork. (Crosby *et al.* 1983)
- Pleuridium nervosum* (Hook.) Mitt. (Tixier, 1979b; Crosby *et al.*, 1983)
- Entodontaceae**
- Campyodontium flavescens* var. *viride* Cardot (Crosby *et al.*, 1983) **End**, Type – Plateau central, environs de Tananarive, *Sibree*, holotype BM#
- Entodon corbieri* Renauld *et* Cardot (Crosby *et al.*, 1983; Tixier, 1995) **End**, Type – Montagne d'Ambre, près de Diégo-Suarez, *Leloutre*, holotype CHE#
- Entodon felicis* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Fianarantsoa (zone du Plateau central), *Félix*, holotype PC.
- Entodon felicis* var. *julaceus* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Plateau central, Ambohimahatsara, près d'Ambositra, *Berthieu*, herb (N.S.).
- Entodon madagassus* Geh. (Crosby *et al.*, 1983) **End**, Type – Ambatondrazaka, *Borgen 100*, holotype PC.

Entodon rutenbergii Geh. (Crosby *et al.*, 1983) **End**, Type – Mont Ankaratra, *Borgen 101*, holotype PC.

Erythrodontium lacoutourei Renaud *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Fianarantsoa, 1905, *Villaume*, holotype BM#

Mesonodon flavescens (Hook.) W.R. Buck (Crosby *et al.*, 1983)

Erpodiaceae

Erpodium beccarii Müll.Hal. *ex* Venturi var. *beccarii* (Tixier, 1979b; Crosby *et al.*, 1983)

Erpodium madagassum Paris *et* Renaud (Crum, 1972; Crosby *et al.*, 1983) **End**, Type – Antsirabe, vallée de la rivière Andrantsay, *Galison*, PC, holotype (N.S.).

Eustichiaceae

Eustichia longirostris (Brid.) Brid. (Crosby *et al.*, 1983)

Fabroniaceae

Fabronia campenonii Renaud *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Forêt d'Amperifery, alt. 1300 m, 06/1890, *Campenon*, holotype PC.

Fabronia crassiretis Renaud *et* Cardot (Crosby *et al.*, 1983)

Fabronia fastigiata Renaud *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Fianarantsoa, 1891, *Besson*, holotype PC.

Fabronia fastigiata var. *asperula* Renaud *et* Paris (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, cercle militaire des Bariï, secteur d'Ivondro, 18/11/1900, *Croll*, holotype PC.

Fabronia garnieri (Paris *et* Renaud) Renaud *et* Paris (Crosby *et al.*, 1983) **End**, Type – Betafo, rive de la Mania, 1902, holotype PC.

Fabronia lachenaudii Renaud (Crosby *et al.*, 1983) **End**, Type – District de Fihaonana, 3/1901, *Ab indig. Coll 30*, holotype PC.

Fabronia motelayi Renaud *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Tananarive, dans les jardins de la Résidence, sur les troncs, 15/04/1897, *Dorr*, holotype PC.

Fabronia villaumii Renaud *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Fianarantsoa, 1905, *Villaume 722*, holotype PC.

Rhizofabronia persoonii var. *sphaerocarpa* (Dusén) Bizot *ex* Ochyra (Crosby *et al.*, 1983; Touw, 1993)

Fissidentaceae

Fissidens angustifolius Sull. (Bruggeman-Nannenga, 2009; Bruggeman-Nannenga & Arts, 2010)

Fissidens aristifer Brugg.-Nann. (Bruggeman-Nannenga, 2009)

Fissidens asplenioides Hedw. (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)

Fissidens bogosicus Müll.Hal. *in* Venturi (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)

Fissidens borgenii Hampe (Bruggeman-Nannenga, 1993)

Fissidens crispulus Brid. (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)

**Fissidens cryptarum* Müll.Hal. – Tampolo Tamatave, littoral forest base of tree, earthen insect nest, ant or termit, S 17°16' E 49°24', 26/10/1972, *M.R. & C.A Crosby 6700, 6702, 6697*, TAN.

Fissidens cryptoneuron P. de la Varde (Crosby *et al.*, 1983)

- Fissidens curvatus* Hornsch. var. *curvatus* (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)
- **Fissidens cyathaeicola* Brugg.Nann. – Marojejy National Park, On tree fern 220 m up trail from camp Mantella, alt. 464 m, 24/11/2009, *Wilding 4*, det. Bruggeman-Nannenga; Marojejy National Park, on tree fern 300 m up trail from camp Mantella, alt. 465 m, 24/11/09, *Wilding 6*, det. Bruggeman-Nannenga.
- Fissidens darntyi* Schimp. (Crosby *et al.*, 1983)
- Fissidens ellipticus* Besch. (Crosby *et al.*, 1983)
- Fissidens flaccidus* Mitt. (Bruggeman-Nannenga, 2009)
- Fissidens grainvillei* Thér. (Crosby *et al.*, 1983) **End**, Type – Kiangara, sur écorces, en très petite quantité, 1931, *Grainville*, holotype PC.
- Fissidens hookerioides* Bizot et Onr. (Crosby *et al.*, 1983) **End**, Type – Tananarive, domaine des Frères de Soavimbahoaka, sur latérite ombragée, alt. 1400 m, 06/07/1971, *Onraedt 71M5137*, holotype PC.
- Fissidens hymenodon* Besch. (Crosby *et al.*, 1983)
- Fissidens inclusus* Bizot et Dury ex Pócs (Bruggeman-Nannenga, 2009)
- Fissidens intramarginatus* (Hampe) A. Jaeger (Bizot, 1974; Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)
- Fissidens leucocinctus* Hampe (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)
- Fissidens madecassus* Müll.Hal. (Crosby *et al.*, 1983; Bruggeman-Nannenga, 2009; Bruggeman-Nannenga & Arts, 2010)
- Fissidens mariei* (Besch.) Broth. (Crosby *et al.*, 1983) **End**, Type – Nosy Be, forêt de Lokobe, 04/1879, *Marie*, holotype PC.
- Fissidens motelayi* Renaud et Cardot (Crosby *et al.*, 1983) **End**, Type – Andriba, 1897, *Dorr*, holotype PC.
- Fissidens ovatus* Brid. (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)
- Fissidens pellucidus* Hornsch. var. *pellucidus* (Crosby *et al.*, 1983; Delgadillo, 1995; Bruggeman-Nannenga, 2010)
- Fissidens planifrons* Besch. (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)
- Fissidens platyneuros* Renaud et Cardot (Crosby *et al.*, 1983) **End**, Type – Andevoranto, 1895, *Perrot*, holotype PC.
- Fissidens plumosus* Hornsch. (Bruggeman-Nannenga & Arts, 2010)
- Fissidens pocsii* Bizot et Dury ex Pócs (Bruggeman-Nannenga, 2009; Bruggeman-Nannenga & Arts, 2010)
- Fissidens punctulatus* Sande Lac. (Bruggeman-Nannenga & Arts, 2010)
- Fissidens ramulosus* Mitt. (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)
- Fissidens reflexus* Hampe (Crosby *et al.*, 1983; Bruggeman-Nannenga, 2009)
- Fissidens rosulatus* P. de la Varde (Crosby *et al.*, 1983) **End**, Type – Tananarive, sur talus, 20/01/1907, *Rotereau*, holotype PC.
- Fissidens rufescens* Hornsch. (Bruggeman-Nannenga, 2009)
- Fissidens sciophyllus* f. *sciophyllus* Mitt. (Crosby *et al.* 1983; Bruggeman-Nannenga, 1993; Bruggeman-Nannenga & Arts, 2010)
- Fissidens scleromitrius* (Besch.) Broth. (Bescherelle, 1891; Crosby *et al.*, 1983)
- Fissidens serratus* Müll.Hal. var. *serratus* (Crosby *et al.*, 1983; Delgadillo, 1995; Bruggeman-Nannenga, 2010)

Fissidens submarginatus Bruch ex C. Krauss (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)

Fissidens subplanifrons Bizot et Onraedt ex Brugg.-Nann (Bruggeman-Nannenga, 2009)

Fissidens subundatus Dury (Crosby *et al.*, 1983)

Fissidens zollingeri Mont. (Crosby *et al.*, 1983; Bruggeman-Nannenga & Arts, 2010)

Funariaceae

Entosthodon borbonicus Besch. (Crosby *et al.*, 1983)

Entosthodon marginatulus Müll. Hal. ex Geh. (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, forêt à l'Est d'Ambatondrazaka, *Rutenberg*, herb (N.S.).

**Entosthodon mauritianus* Schimp. ex Besch. – Befotaka forêt, S 18°56'47" E 47°06'03", 16/08/1926, *Decary 77*, holotype MO.

Entosthodon renauldii Thér. (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, pays Betsileo, 2/1905, *Villaume*, holotype PC, isotype PC, BM.

Funaria decaryi Thér. (Crosby *et al.*, 1983) **End**, Type – Ambovombe, Fort-Dauphin, *Decary*, holotype S.

Funaria delicatula Thér. (Crosby *et al.*, 1983) **End**, Type – Environ de Tananarive, *Perrier de la Bathie*, holotype PC.

Funaria hygrometrica var. *calvescens* (Schwaegr.) Kindb. (Crosby *et al.*, 1983; Pócs & Geissler, 2002)

Funaria imerinensis Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Imerina, dans un gazon de *Webera decurrens* Ren. & Card, *Villaume*, holotype PC.

Funaria subleptopoda Hampe (Crosby *et al.*, 1983) **End**, Type – Imerina, 2/9/1847, *Borgen*, holotype PC.

Physcomitrium coarctatum Cardot (Crosby *et al.*, 1983)

Physcomitrium dilatatum Renauld et Cardot (Crosby *et al.*, 1983) **End**, Type – Environ de Tananarive, in terra, *Camboué*, holotype PC.

Gigaspermaceae

Gigaspermum repens (Hook.) Lindb. (Tixier, 1979b; Crosby *et al.*, 1983)

**Oedipodiella australis* (Wager & Dixon) Dixon – Morondava, forêt, alt. 20 m, 11/04/1979, *Tixier 12114*, TAN.

Grimmiaceae

Grimmia elatior Bruch ex Bals.-Criv. et De Not. (Crosby *et al.*, 1983)

Grimmia elongata Kaulf. (Crosby *et al.*, 1983)

Grimmia longirostris Hook. (Muñoz, 1998)

Bucklandiella membranaceum (Mitt.) Paris (Crosby *et al.*, 1983)

Hedwigiaceae

**Braunia secunda* (Hook.) Bruch et Schimp. – Station forestière de Manjakatempo, rocher, alt. 2600 m, 22/08/1971, *Cremers 1705*, TAN; Ankaratra, sur rocher, 27/03/1972, *Cremers 1957*, TAN; Ankaratra, sur rocher, basaltique, 08/1955, *Bosser 8208*, TAN.

Bryowijkia madagassa Touw (Touw, 1993)

Hedwigia ciliata (Hedw.) Ehrh. ex P. Beauv. var. *ciliata* (Crosby *et al.*, 1983)

Hypnaceae

- Ectropothecium chenagonii* Renaud *et* Cardot (Crosby *et al.*, 1983)
Ectropothecium chenagonii var. *hamatulum* Renaud & Cardot (Crosby *et al.*, 1983) **End**, Type – Entre Vinanitelo et Ikongo, 1892, *Besson*, holotype PC.
Ectropothecium intertextum Renaud *et* Cardot (Crosby *et al.*, 1983)
Ectropothecium mauritianum Renaud *et* Cardot (Crosby *et al.*, 1983)
Ectropothecium occultum Renaud *et* Cardot (Crosby *et al.*, 1983)
Ectropothecium ovalifolium (Besch.) W.R. Buck (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Nosy Be, forêt de Lokobe, *Marie*, herb (N.S.).
Ectropothecium paillotii Renaud *et* Cardot (Crosby *et al.*, 1983)
Ectropothecium perrieri Thér. (Crosby *et al.*, 1983) **End**, Type – Massif de l'Andringitra, alt. 1600 m, 1921, *Perrier de la Bathie*, holotype PC.
Ectropothecium perrotii Renaud *et* Cardot (Crosby *et al.*, 1983)
Ectropothecium regulare (Brid.) A. Jaeger (Crosby *et al.*, 1983)
Ectropothecium seychellarum Besch. (Crosby *et al.*, 1983)
Ectropothecium tamatavense Broth. (Crosby *et al.*, 1983)
Gammiella ceylonensis (Broth.) B.C. Tan *et* W.R. Buck (Crosby *et al.*, 1983)
Glossadelphus guineensis (Broth. *et* Paris) Crosby, B.H. Allen *et* Magill (Crosby *et al.*, 1983)
Glossadelphus semiscabrus (Renaud *et* Cardot) Crosby *et al.* (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, environs d'Andevoranto, 1895, *Perrot*, holotype PC.
Glossadelphus viridis (Renaud *et* Cardot) Crosby *et al.* (Crosby *et al.*, 1983) **End**, Type – Diégo-Suarez, Montagne d'Ambre, *Chénagon*, holotype PC.
Hypnum jutlandicum Holmen *et* E. Warncke (Crosby *et al.*, 1983)
Hypnum macrogynum Besch. (Crosby *et al.*, 1983)
Mittenothamnium horridulum (Broth.) Cardot (Crosby *et al.*, 1983)
Mittenothamnium lacouturei (Renaud *et* Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Betsileo, province d'Ambositra, 1906, *Villaume*, holotype BM#
Mittenothamnium limosum (Besch.) Cardot (Crosby *et al.*, 1983)
Mittenothamnium madagassum (Besch.) Cardot (Crosby *et al.*, 1983; Een, 1997)
Mittenothamnium microthamnioides (Geh.) Wijk *et* Margad. (Crosby *et al.*, 1983; Een, 1997)
Mittenothamnium microthamnioides var. *glauculum* (Cardot) Wijk *et* Margad. (Crosby *et al.*, 1983) **End**, Type – Forêt de Manongarivo, *Drouhard*, holotype PC#
Mittenothamnium reptans (Hedw.) Cardot (Crosby *et al.*, 1983)
Phyllocladon scutellifolius (Besch.) W.R. Buck (Crosby *et al.*, 1983; O'Shea & Buck, 2001) **End**, Type – Nosy Komba, associé à *Hookeria nossiana*, 08/1879, *Marie s.n.*, holotype BM.
Phyllocladon truncatulus (Welw. *et* Duby) W.R. Buck (Crosby *et al.*, 1983)
Rhacopilopsis trinitensis (Müll.Hal.) E. Britton *ex* Dixon (Crosby *et al.*, 1983)
Rhacopilopsis variegata (Welw. *et* Duby) M.C. Watling *et* O'Shea (Buck, 1993; Watling & O'Shea, 2000)
Taxiphyllum taxirameum (Mitt.) M. Fleisch. (Crosby *et al.*, 1983)

Hypnaceae

- Ectropothecium chenagonii* Renaud et Cardot (Crosby *et al.*, 1983)
Ectropothecium chenagonii var. *hamatulum* Renaud & Cardot (Crosby *et al.*, 1983) **End**, Type – Entre Vinanitelo et Ikongo, 1892, *Besson*, holotype PC.
Ectropothecium intertextum Renaud et Cardot (Crosby *et al.*, 1983)
Ectropothecium mauritianum Renaud et Cardot (Crosby *et al.*, 1983)
Ectropothecium occultum Renaud et Cardot (Crosby *et al.*, 1983)
Ectropothecium ovalifolium (Besch.) W.R. Buck (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Nosy Be, forêt de Lokobe, *Marie*, herb (N.S.).
Ectropothecium pailloii Renaud et Cardot (Crosby *et al.*, 1983)
Ectropothecium perrieri Thér. (Crosby *et al.*, 1983) **End**, Type – Massif de l'Andringitra, alt. 1600 m, 1921, *Perrier de la Bathie*, holotype PC.
Ectropothecium perrotii Renaud et Cardot (Crosby *et al.*, 1983)
Ectropothecium regulare (Brid.) A. Jaeger (Crosby *et al.*, 1983)
Ectropothecium seychellarum Besch. (Crosby *et al.*, 1983)
Ectropothecium tamatavense Broth. (Crosby *et al.*, 1983)
Gammiella ceylonensis (Broth.) B.C. Tan et W.R. Buck (Crosby *et al.*, 1983)
Glossadelphus guineensis (Broth. et Paris) Crosby, B.H. Allen et Magill (Crosby *et al.*, 1983)
Glossadelphus semiscabrus (Renaud et Cardot) Crosby *et al.* (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, environs d'Andevoranto, 1895, *Perrot*, holotype PC.
Glossadelphus viridis (Renaud et Cardot) Crosby *et al.* (Crosby *et al.*, 1983) **End**, Type – Diégo-Suarez, Montagne d'Ambre, *Chénagon*, holotype PC.
Hypnum jutlandicum Holmen et E. Warncke (Crosby *et al.*, 1983)
Hypnum macrognum Besch. (Crosby *et al.*, 1983)
Mittenothamnium horridulum (Broth.) Cardot (Crosby *et al.*, 1983)
Mittenothamnium lacouturei (Renaud et Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Betsileo, province d'Ambositra, 1906, *Villaume*, holotype BM#
Mittenothamnium limosum (Besch.) Cardot (Crosby *et al.*, 1983)
Mittenothamnium madagassum (Besch.) Cardot (Crosby *et al.*, 1983; Een, 1997)
Mittenothamnium microthamnioides (Geh.) Wijk et Margad. (Crosby *et al.*, 1983; Een, 1997)
Mittenothamnium microthamnioides var. *glauculum* (Cardot) Wijk et Margad. (Crosby *et al.*, 1983) **End**, Type – Forêt de Manongarivo, *Drouhard*, holotype PC#
Mittenothamnium reptans (Hedw.) Cardot (Crosby *et al.*, 1983)
Phyllodon scutellifolius (Besch.) W.R. Buck (Crosby *et al.*, 1983; O'Shea & Buck, 2001) **End**, Type – Nosy Komba, associé à *Hookeria nossiana*, 08/1879, *Marie s.n.*, holotype BM.
Phyllodon truncatulus (Welw. et Duby) W.R. Buck (Crosby *et al.*, 1983)
Rhacopilopsis trinitensis (Müll.Hal.) E. Britton ex Dixon (Crosby *et al.*, 1983)
Rhacopilopsis variegata (Welw. et Duby) M.C. Watling et O'Shea (Buck, 1993; Watling & O'Shea, 2000)
Taxiphyllum taxirameum (Mitt.) M. Fleisch. (Crosby *et al.*, 1983)

- Vesicularia alboviridis* var. *rufula* (Renauld *et* Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Diégo-Suarez, *Chénagon*, holotype PC.
- Vesicularia ayresii* (Besch.) Broth. (Crosby *et al.*, 1983)
- Vesicularia combae* (Renauld *et* Cardot) Broth. (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Nosy Komba, *Marie*, holotype PC#
- Vesicularia crassiramea* (Renauld *et* Cardot) Broth. (Crosby *et al.*, 1983)
- Vesicularia crassiramea* var. *laxifolia* (Renauld *et* Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Zone des savanes occidentales, cercle de Maintirano, holotype PC.
- Vesicularia galerulata* (Duby) Broth. (Crosby *et al.*, 1983)
- Vesicularia galerulata* var. *subpilligera* (Renauld *et* Paris) Wijk *et* Margad. (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Betafo, rive droite de la Mania, 1901, *Galison*, holotype PC.
- Vesicularia hygrobium* (Besch.) Broth. (Crosby *et al.*, 1983)
- Vesicularia immunda* (Renauld) Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Imerina oriental, *Hildebrandt*, herb (N.S.).
- Hypopterygiaceae**
- Hypopterygium tamarisci* (Sw. *ex* Sw.) Brid. *ex* Müll.Hal. (Crosby *et al.*, 1983; Kruijjer 1997; Kruijjer, 2002)
- Lopidium struthiopteris* (Brid.) M. Fleisch. (Crosby *et al.*, 1983; Kruijjer, 1997; Kruijjer, 2002)
- Leptodontaceae**
- Leptodon fuciformis* (Brid.) Enroth (Crosby *et al.*, 1983)
- Leskeaceae**
- Pseudoleskea obtusiuscula* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Fianarantsoa, troncs d'arbres, 1904, *Villaume*, holotype BM!, isotype PC.
- Leucobryaceae**
- Atractylocarpus madagascariensis* (Thér.) Padberg *et* J.-P. Frahm (Crosby *et al.*, 1983)
- Campylopus arctocarpus* (Besch.) J.-P. Frahm subsp. *madecassus* (Crosby *et al.*, 1983, Frahm, 1985)
- Campylopus arcuatus* (Brid.) A. Jaeger (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus aureonitens* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus cambouei* Renauld *et* Cardot (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus catarractilis* (Müll.Hal.) Paris (Frahm, 1985)
- Campylopus crateris* Besch. (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus decaryi* Thér. (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus filifolius* (Hornsch.) Mitt. (Crosby *et al.*, 1983; Een, 1993)
- Campylopus flaccidus* Renauld *et* Cardot (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus flexuosus* (Hedw.) Brid. var. *flexuosus* (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus hildebrandtii* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983)
- Campylopus jamesonii* (Hook.) A. Jaeger (Crosby *et al.*, 1983; Frahm, 1985)
- Campylopus julaceus* (Renauld *et* Cardot) J.-P. Frahm subsp. *arboastii* (Crosby *et al.*, 1983; Frahm, 1985)

- Campylopus nanophyllus* Müll.Hal. ex Broth. (Crosby *et al.*, 1983)
Campylopus nivalis (Brid.) Brid. var. *nivalis* (Frahm, 1985)
Campylopus perpusillus Mitt. (Crosby *et al.*, 1983; Frahm, 1985)
Campylopus pilifer Brid. subsp. *pilifer* (Crosby *et al.*, 1983; Frahm, 1985)
Campylopus pseudobicolor Müll.Hal. ex Renauld & Cardot (Crosby *et al.*, 1983; Frahm, 1985)
Campylopus robillardei Besch. (Crosby *et al.*, 1983; Frahm, 1985; Pócs & Geissler, 2002)
Campylopus schmidii (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983; Frahm, 1985)
Campylopus smaragdinus (Brid.) A. Jaeger (Crosby *et al.*, 1983; Frahm, 1985)
Campylopus thwaitesii (Mitt.) A. Jaeger (Crosby *et al.*, 1983; Frahm, 1985)
Campylopus trachyblepharon (Renauld et Cardot) J.-P. Frahm subsp. *comatus* (Crosby *et al.*, 1983; Frahm, 1985)
Leucobryum acutifolium (Mitt.) Cardot (Crosby *et al.*, 1983)
Leucobryum boivinianum Besch. (Crosby *et al.*, 1983)
Leucobryum boryanum Besch. (Crosby *et al.*, 1983)
Leucobryum boryanum var. *minus* Cardot (Crosby *et al.*, 1983) **End**, Type – Pays Betsileo, sineloco, *Montaul*, herb (N.S.).
Leucobryum cambouei Cardot (Crosby *et al.*, 1983) **End**, Type – *Camboué*, herb (N.S.).
Leucobryum comorense Müll.Hal. (Crosby *et al.*, 1983; Pócs & Geissler, 2002)
Leucobryum cucullatum Broth. (Crosby *et al.*, 1983)
Leucobryum cucullatum var. *rutenbergii* (Geh.) Cardot (Crosby *et al.*, 1983)
Leucobryum galinonii Cardot et Paris (Crosby *et al.*, 1983) **End**, Type – Betafo, rive droite de la Mania, *Galison*, holotype PC#
Leucobryum heterodictyon Besch. (Bescherelle, 1891; Crosby *et al.*, 1983) **End**, Type – Sainte Marie, *Marie Edouard Auguste*, holotype PC.
Leucobryum heterodictyon var. *microphyllum* (Cardot) Wijk et Margad. (Crosby *et al.*, 1983) **End**, Type – Ile Sainte Marie, *Marie*, holotype PC#
Leucobryum isleanum Besch. (Crosby *et al.*, 1983)
Leucobryum isleanum var. *molle* (Müll.Hal.) Cardot (Crosby *et al.*, 1983)
Leucobryum madagassum Besch. (Crosby *et al.*, 1983)
Leucobryum mayottense Cardot (Crosby *et al.*, 1983)
Leucobryum parvulum Cardot (Crosby *et al.*, 1983, Pócs & Geissler, 2002) **End**, Type – holotype PC.
Leucobryum perrotii Renauld et Cardot (Crosby *et al.*, 1983, Pócs & Geissler, 2002)
Leucobryum pseudomadagassum Cardot (Crosby *et al.*, 1983) **End**, Type – Zone supérieure des forêts, Imerina, Andrangoloaka, *Hildebrandt*, holotype PC.
Leucobryum sanctae-mariae Cardot (Crosby *et al.*, 1983, Pócs & Geissler, 2002) **End**, Type – Ile Sainte Marie, *Marie*, holotype PC.
Ochrobryum sakalavum Cardot et Paris (Crosby *et al.*, 1983; Allen, 1992; Pócs & Geissler, 2002) **End**, Type – cercle de Maintirano, poste d'Ampoza, près du village de Tahotofoly, sur bois pourri, holotype PC!
- Leucodontaceae**
Leucodon canariensis (Brid.) Schwaegr. (Crosby *et al.*, 1983)
Leucodon rutenbergii Müll.Hal. ex Geh. (Crosby *et al.*, 1983)

Pterogoniadelphus assimilis (Müll.Hal.) Ochyra *et* Zijlstra (Crosby *et al.*, 1983)

Pterogonium gracile (Hedw.) Sm. (Crosby *et al.*, 1983)

Pterogonium gracile var. *madagassum* (Geh.) M. Fleisch. (Crosby *et al.*, 1983)

Leucomiaceae

Leucomium strumosum (Hornsch.) Mitt. (Crosby *et al.*, 1983; Allen, 1987; Pócs & Geissler, 2002)

Meteoriaceae

Aerobryopsis capensis (Müll.Hal.) M. Fleisch. (Crosby *et al.*, 1983)

Barbella capillicaulis (Renauld *et* Cardot) Cardot var. *capillicaulis* (Crosby *et al.*, 1983)

Floribundaria floribunda (Dozy *et* Molk.) M. Fleisch. (Crosby *et al.*, 1983)

Floribundaria floribunda var. *madagassa* (Renauld *et* Cardot) Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Forêt d'Ambohitombo, *Forsyth Major*, FH; Fianarantsoa, plateau d'Ikongo, entre Savondronina *et* Ranomafana, *et* entre Vinanitelo *et* Ikongo, *Besson*, holotype (N.S.).

Floribundaria floribundula (Müll.Hal.) M. Fleisch. (Crosby *et al.*, 1983)

Floribundaria vaginans (Welw. *et* Duby) Broth. (Crosby *et al.*, 1983)

Papillaria africana (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983)

Papillaria africana var. *gracilis* (Renauld *et* Cardot) Wijk *et* Margad. (Crosby *et al.*, 1983) **End**, Type – Diégo-Suarez, 1890, *Chenagon*; Entre Vinanitelo *et* Ikongo, 1892, *Besson*. Betsileo, sine loco, *Rev. Montaut*; Entre Savondronina *et* Ranomafana, 1892, *Besson*, holotype (N.S.).

Papillaria borchgrevinkii Kiaer (Crosby *et al.*, 1983)

Papillaria flaccidula Cardot (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, forêt d'Analamazaotra, *Camboué*, herb (N.S.).

Papillaria perichaetialis (Hampe) A. Jaeger (Crosby *et al.*, 1983) **End**, Type – Analamazaotra, 1871, *Borchgrewink 17*, holotype BM.

Trachypodopsis serrulata (P. Beauv.) M. Fleisch. var. *serrulata* (Van Zanten, 1959; Crosby *et al.*, 1983; Pócs & Geissler, 2002)

Trachypus appendiculatus (Renauld *et* Cardot) Broth. (Van Zanten, 1959; Crosby *et al.*, 1983)

Trachypus bicolor var. *viridulus* (Mitt.) Zanten (Van Zanten, 1959; Crosby *et al.*, 1983)

Meesiaceae

Leptobryum pyriforme (Hedw.) Wilson (Crosby *et al.*, 1983)

Mniaceae

Epipterygium diversifolium Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone des savanes occidentales, cercle de Maintirano, 1901, *Collecteur indigène*, holotype PC.

Mielichhoferia cardotii A.J. Shaw *et* H.A. Crum (Crosby *et al.*, 1983) **End**, Type – Zone de plateau central, Ambohipo, *Camboué*, herb (N.S.).

Mielichhoferia madagassa var. *gracilis* Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Angavokely, alt. 1800 m, 1924, *Drouhard*, holotype PC.

Plagiomnium rhynchophorum (Hook.) T.J. Kop. var. *rhynchophorum* (Koponen, 1981; Crosby *et al.*, 1983)

Pohlia baronii Wijk *et* Margad. (Crosby *et al.*, 1983)

Pohlia elongata Hedw. var. *elongata* (Crosby *et al.*, 1983; Delgadillo, 1995)

- Pohlia heribaudii* var. *madagassa* (Renauld *et* Cardot) Wijk *et* Margad. (Crosby *et al.*, 1983)
- Pohlia lacouturei* (Thér.) O'Shea (Crosby *et al.*, 1983) **End**, Type – Pays des Betsileo, sur gneiss en décomposition, *Villaume & Lacouture*, herb (N.S.).
- Pseudopohlia microstoma* (Harv.) Mizush. (Crosby *et al.*, 1983)
- Schizymenium commixtum* (Thér.) A.J. Shaw (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, forêt à sous-bois herbacé, alt. 1200-2400 m, *Perrier de la Bathie*, holotype PC.
- Schizymenium madagassum* (Renauld *et* Cardot *ex* Cardot) A.J. Shaw (Crosby *et al.*, 1983) **End**, Type – Mont Angavokely, Est Antananarivo, alt. 1800 m, 1924, *Drouhard*, holotype PC.
- Neckeraceae**
- Homaliodendron exiguum* (Bosch *et* Sande Lac.) M. Fleisch. (Crosby *et al.*, 1983)
- Homaliodendron piniforme* (Brid.) Enroth (Crosby *et al.*, 1983; Enroth, 1993)
- Neckera remota* Bruch *et* Schimp. *ex* Müll.Hal. (Crosby *et al.*, 1983)
- Neckera valentiniana* Besch. (Crosby *et al.*, 1983)
- Neckeropsis boiviniana* (Besch.) Cardot (Crosby *et al.*, 1983)
- **Neckeropsis disticha* (Hedw.) Kindb. – Brickaville, large trees next to shallow rive, S 18°55' E 48°34', alt. 450 m, 23/10/1972, *M.R. & C.A Crosby 6754*, TAN.
- Neckeropsis lepineana* (Mont.) M. Fleisch. (Crosby *et al.*, 1983)
- Neckeropsis madecassa* (Besch.) M. Fleisch. (Crosby *et al.*, 1983)
- Orthostichidium pentastichum* (Brid.) B.H. Allen *et* Magill. (Crosby *et al.*, 1983; Allen & Magill, 2007)
- Orthostichella rigida* (Müll.Hal.) B.H. Allen *et* Magill. (Allen & Magill, 2007)
- Orthostichella versicolor* (Müll.Hal.) B.H. Allen *et* Magill. (Crosby *et al.*, 1983; Allen & Magill, 2007)
- Orthostichella longinervis* (Renauld *et* Cardot) B.H. Allen *et* Magill. (Allen & Magill, 2007)
- Orthostichella welwitschii* (Duby) B.H. Allen *et* Magill. (Allen & Magill, 2007)
- Pilotrichella flexilis* (Hedw.) Aongstr. (Crosby *et al.*, 1983; Allen & Magill, 2003)
- Pilotrichella flexilis* f. *nudiramulosa* (Müll.Hal.) B.H. Allen *et* Magill (Allen & Magill, 2003)
- Pilotrichella mascarenica* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983; Allen & Magill, 2003)
- Pilotrichella pseudo-imbricata* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983)
- Pinnatella minuta* (Mitt.) Broth. (Crosby *et al.*, 1983; Enroth, 1994)
- Porotrichum elongatum* (Welw. *et* Duby) A. Gepp (De Sloover, 1983)
- Porotrichum madagassum* Kiaer *ex* Besch. (De Sloover, 1983)
- Porotrichum stipitatum* (Mitt.) W.R. Buck (De Sloover, 1983)
- Porotrichum usagarum* Mitt. (De Sloover, 1983)
- Porotrichum variifolioides* (De Sloover) Enroth (De Sloover, 1983)
- Thamnobryum malgachum* (Cardot) O'Shea (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, forêt de Manongarivo, 1909, *Drouhard*, holotype PC.
- Orthotrichaceae**
- Cardotiella appendiculata* (Renauld *et* Cardot) Vitt (Crosby *et al.*, 1983; Goffinet, 1996)

- Cardotiella elimbata* (Thér.) Goffinet (Crosby *et al.*, 1983; Goffinet, 1996) **End**, Type – Farafangana, sur souche d'arbre, en forêt, *Decary*, holotype PC, isotype S.
- Cardotiella renauldii* (Broth.) Vitt. (Crosby *et al.*, 1983; Goffinet, 1996) **End**, Type – holotype PC.
- Cardotiella subappendiculata* (Broth.) Vitt (Crosby *et al.*, 1983)
- Groutiella laxotorquata* (Besch.) Wijk *et* Margad. (Crosby *et al.*, 1983)
- Macrocoma tenuis* (Hook. *et* Grev.) Vitt subsp. *tenuis* (Crosby *et al.*, 1983)
- Macromitrium adelphinum* Cardot (Crosby *et al.*, 1983) **End**, Type – Forêt d'Amperifery, *Campeyon*, herb (N.S.).
- Macromitrium ancistrophyllum* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone supérieure des forêts, Ankeramadinika, *Borgen 202*, holotype BM.
- Macromitrium anomodictyon* Cardot (Crosby *et al.*, 1983) **End**, Type – District d'Andramasina, entre Tsinjoarivo & Ambohimasina, dans un petit bois, sur branche d'arbre, alt. 1700 m, 02/12/1912, *Viguié 1932*, holotype PC.
- Macromitrium calocalyx* Geh. (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, forêt à l'est d'Ambatondrazaka, *Rutenberg*, herb (N.S.).
- Macromitrium fasciculare* Mitt. (Crosby *et al.*, 1983)
- Macromitrium fasciculare* var. *angustifolium* P. de la Varde (Crosby *et al.*, 1983) **End**, Type – Sommet oriental du Massif de Marojejy, à l'Ouest de la Haute Manténina, affluent de la Lokoho, gneiss et quartzite, alt. 1850 m, 26/3/1949, *Humbert*, holotype PC.
- Macromitrium fimbriatum* (P.Beauv.) Schwaegr. (Crosby *et al.*, 1983)
- Macromitrium mauritianum* Schwaegr. (Crosby *et al.*, 1983)
- Macromitrium nanothecium* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone supérieure des forêts, Andrangoloaka, *Hildebrandt*, holotype FH.
- Macromitrium nanothecium* var. *sublaeve* Thér. (Crosby *et al.*, 1983) **End**, Type – Fort-Dauphin, sur écorce, *Decary*, holotype PC!
- Macromitrium onraedtii* Bizot (Bizot, 1974; Crosby *et al.*, 1983) **End**, Type – Entre Foulpointe et Andondabe, au Nord de Tamatave, sur un arbre d'une forêt sur sable, 12/05/1972, *Cremers 2165*, holotype PC.
- Macromitrium orthostichum* Nees *ex* Schwägr. (Crosby *et al.*, 1983)
- Macromitrium proximum* Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, alt. 1200 m, 04/1924, *Perrier de la Bathie*, holotype PC.
- Macromitrium rhizomatosum* Müll.Hal. (Crosby *et al.*, 1983) **End**, Type – Nosy Be, *Pervillé 789*, holotype PC.
- Macromitrium sanctae-mariae* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Sainte Marie, 1893, *Darbould*, holotype PC.
- Macromitrium sclerodictyon* Cardot (Crosby *et al.*, 1983)
- Macromitrium semipapillosum* Thér. *et* P. de la Varde (Crosby *et al.*, 1983) **End**, Type – 1922, *Carrougeau*, holotype PC.
- Macromitrium serpens* (Bruch *ex* Hook. & Grev.) Brid. (Crosby *et al.*, 1983)
- Macromitrium soulae* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Ambositra, Betsileo, 1890, *Soula*, holotype PC.
- Macromitrium subpungens* Hampe *ex* Müll.Hal. (Crosby *et al.*, 1983)
- Macromitrium subpungens* var. *madagassum* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Maroantsetra dans la baie d'Antongil, *Mathieu*, herb (N.S.).

- Macromitrium subtortum* (Hook. et Grev.) Schwaegr. (Crosby *et al.*, 1983) **End**, Type – unknown.
- Macromitrium sulcatum* (Hook.) Brid. var. *sulcatum* (Crosby *et al.*, 1983; Ellis & Wilbraham, 2008)
- Macromitrium urceolatulum* Müll.Hal. ex Geh. (Crosby *et al.*, 1983)
- Schlotheimia acutifolia* Renaud et Paris (Crosby *et al.*, 1983) **End**, Type – Forêt d’Ambohitantely, 1901, *Collecteur indigène*, holotype PC.
- Schlotheimia acutifolia* var. *angustifolia* Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, forêt à sous bois herbacé, alt. 1200-2400 m, *Perrier de la Bathie*, holotype PC.
- Schlotheimia badiella* Besch. (Crosby *et al.*, 1983)
- Schlotheimia badiella* var. *helicophylla* Besch. (Crosby *et al.*, 1983)
- Schlotheimia boiviniana* Besch. (Crosby *et al.*, 1983)
- Schlotheimia conica* Renaud et Cardot (Crosby *et al.*, 1983) **End**, Type – Environs de la forêt d’Ambatovory, alt. 1400 m, 1889, *Camboué*, holotype PC.
- Schlotheimia excorugata* Müll.Hal. ex Cardot (Crosby *et al.*, 1983)
- Schlotheimia fornicata* Duby (Crosby *et al.*, 1983)
- Schlotheimia fornicata* var. *apiculata* P. de la Varde (Crosby *et al.*, 1983) **End**, Type – Pentes orientale du massif de Marojejy, à l’ouest de la rivière Manantenina, affluent de la Lokoho, sylvie à lichens sur gneiss et quartzite, alt. 1400 m, 15/12/1948, *Humbert*, holotype PC.
- Schlotheimia fornicata* var. *microtheca* P. de la Varde (Crosby *et al.*, 1983) **End**, Type – Vallée de la Lokoho Nord-Est, mont Beondroka, au nord de Maroambihy, rochers de la crête (gneiss et quartzite), alt. 1400 m, 17/03/1949, *Humbert*, holotype PC.
- Schlotheimia foveolata* Renaud et Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Ile de Sainte Marie sur les bords de la rivière Fitarihana, 1893, *Darbould*, holotype PC.
- Schlotheimia foveolata* var. *torquescens* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Imerina, environ de Tananarive, *Camboué & Sibree*, holotype BM.
- Schlotheimia gauthieri* Thér. (Crosby *et al.*, 1983)
- Schlotheimia malacophylla* Besch. (Crosby *et al.*, 1983)
- Schlotheimia microcarpa* Geh. (Crosby *et al.*, 1983)
- Schlotheimia microphylla* Besch. (Crosby *et al.*, 1983)
- Schlotheimia nossi-beana* Müll.Hal. (Crosby *et al.*, 1983) **End**, Type – Nosy Be, 1841, *Pervillé*, holotype PC.
- Schlotheimia nossi-beana* var. *linealis* (Geh.) Thér. (Crosby *et al.*, 1983) **End**, Type – Nosy Be, *Boivin*, holotype PC.
- Schlotheimia pauli* Renaud et Cardot (Crosby *et al.*, 1983) **End**, Type – Antsahambavy, 1902, *Dalincourt*, holotype PC.
- Schlotheimia perrieri* Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, alt. 1200m, 4/1924, *Perrier de la Bathie*, holotype PC.
- Schlotheimia perrotii* Renaud et Cardot (Crosby *et al.*, 1983) **End**, Type – Andevoranto, 1895, *Perrot*, holotype PC.
- Schlotheimia perrotii* var. *breviseta* Thér. (Crosby *et al.*, 1983) **End**, Type – Andevoranto, herb (N.S.).
- Schlotheimia robillardii* Duby (Crosby *et al.*, 1983)
- Schlotheimia robusta* Thér. (Crosby *et al.*, 1983)

- Schlotheimia semidiaphana* (Renauld *et* Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Plateau d’Ikongo, 1892, *Besson 294*, holotype PC.
- Schlotheimia squarrosa* Brid. (Crosby *et al.*, 1983; Delgadillo, 1995)
- Schlotheimia subfornicata* Thér. (Crosby *et al.*, 1983)
- Schlotheimia tenuiseta* Geh. (Crosby *et al.*, 1983) **End**, Type – Ambatondrazaka, herb (N.S.).
- Schlotheimia trichophora* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Entre Ankeramadinika et la forêt d’Analamazaotra, 1891, *Camboué & Campenon*, holotype PC.
- Schlotheimia trichophora* var. *stenophylla* (Renauld *et* Cardot) Thér. (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, pays de Betsileo, *Villaume*, holotype BM.
- Schlotheimia trypanoclada* Geh. (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Alabe, près de Marotandrano, *Rutenberg*, holotype PC.
- Ulota fulva* Brid. (Crosby *et al.*, 1983)
- Zygodon laxifolius* Thér. (Crosby *et al.*, 1983) **End**, Type – Massif d’Andringitra, alt. 1600 m, 1921, *Perrier de la Bathie*, holotype PC.
- Zygodon leptocarpus* Thér. (Crosby *et al.*, 1983) **End**, Type – Massif d’Andringitra, alt. 1600 m, 1921, *Perrier de la Bathie*, holotype PC.
- Zygodon reinwardtii* var. *madacassus* Cardot (Crosby *et al.*, 1983) **End**, Type – NW Madagascar, *Pervillé*, holotype PC.
- Zygodon reinwardtii* (Hornsch.) A. Braun var. *reinwardtii* (Crosby *et al.*, 1983)
- Phyllogoniaceae**
- Phyllogonium viscosum* (P. Beauv.) Mitt. (Crosby *et al.*, 1983)
- Pilotrichaceae**
- Callicostella africana* Mitt. (Crosby *et al.*, 1983)
- Callicostella brevipes* (Broth.) Broth. (Crosby *et al.*, 1983)
- Callicostella constricta* (Müll.Hal.) Kindb. (Crosby *et al.*, 1983)
- Callicostella fissidentella* (Besch.) Kindb. (Crosby *et al.*, 1983)
- Callicostella lacerans* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983)
- Callicostella leptocladula* (Broth.) Broth. (Crosby *et al.*, 1983)
- Callicostella papillata* var. *brevifolia* M. Fleisch. (Crosby *et al.*, 1983)
- Callicostella papillata* (Mont.) Mitt. var. *papillata* (Crosby *et al.*, 1983; Pócs & Geissler, 2002)
- Callicostella parvocellulata* Mitt. (Crosby *et al.*, 1983)
- Callicostella perrotii* (Renauld *et* Cardot *ex* Paris) Broth. (Crosby *et al.*, 1983)
- Callicostella pusilla* Demaret *et* P. de la Varde (Crosby *et al.*, 1983)
- Callicostella seychellensis* (Besch.) Kindb. (Crosby *et al.*, 1983; Pócs & Geissler, 2002)
- Callicostella tristis* (Müll.Hal.) Broth. (Pócs & Geissler, 2002)
- Cyclodictyon aubertii* (P. Beauv.) Kuntze (Crosby *et al.*, 1983)
- Cyclodictyon laetevirens* (Hook. *et* Taylor) Mitt. (Crosby *et al.*, 1983)
- Cyclodictyon vallis-gratiae* (Müll.Hal.) Kuntze (Crosby *et al.*, 1983; Pócs & Geissler, 2002)
- Hookeriopsis diversifolia* (Renauld *et* Cardot) Broth. *ex* Cardot *in* Grandid. (Crosby *et al.*, 1983)
- Lepidopilidium attenuatum* Thér. (Crosby *et al.*, 1983) **End**, Type – Forêt d’Andasibe, sur l’Onive, 02/1925, *Perrier de la Bathie*, holotype PC.

- Lepidopilidium chenagonii* (Renauld *et* Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, montagne d'Ambre, près Diégo-Suarez, *Chénagon*, herb (N.S.).
- Lepidopilidium corbieri* (Renauld *et* Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, montagne d'Ambre, *Leloutre*, holotype CHE.
- Lepidopilidium parvulum* Cardot (Crosby *et al.*, 1983) **End**, Type – NW, *Pervillé*, herb (N.S.).
- Lepidopilidium subrevolutum* (Renauld *et* Cardot) Cardot (Crosby *et al.*, 1983)
- Lepidopilum hirsutum* var. *tuberculatum* Thér. (Crosby *et al.*, 1983) **End**, Type – Andasibe, sur l'Onive, forêt à sous-bois herbacé, alt. 800-1400 m, 02/1925, *Perrier de la Bathie*, holotype PC.
- Lepidopilum lastii* Mitt. (Crosby *et al.*, 1983; Churchill, 1988)
- Lepidopilum verrucipes* Cardot (Crosby *et al.*, 1983; Churchill, 1988)
- Polytrichaceae**
- Atrichum androgynum* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983; De Sloover, 1986)
- Pogonatum belangeri* (Müll.Hal.) A. Jaeger (Hyvönen, 1989; Pócs & Geissler, 2002)
- Pogonatum capense* (Hampe) A. Jaeger (Crosby *et al.*, 1983; Hyvönen, 1989; De Sloover, 1986; Pócs & Geissler, 2002)
- Pogonatum convolutum* (Hedw.) P. Beauv. (Crosby *et al.*, 1983; Hyvönen, 1989; De Sloover, 1986; Pócs & Geissler, 2002)
- Pogonatum gracilifolium* Besch. (Crosby *et al.*, 1983)
- Polytrichastrum formosum* (Hedw.) G.L. Sm. (Crosby *et al.*, 1983)
- Polytrichum commune* Hedw. var. *commune* (Crosby *et al.*, 1983; De Sloover, 1986)
- Polytrichum glabrum* Schrad. (Crosby *et al.*, 1983)
- Polytrichum juniperellum* Geh. (Crosby *et al.*, 1983) **End**, Type – Plateau central, Ambohimaro, Ambatomainty près Tananarive, *Rutenberg*, herb (N.S.).
- Polytrichum subformosum* var. *parvisetum* (Müll.Hal.) Cardot (Crosby *et al.*, 1983) **End**, Type – Plateau central, Imerina, bords du lac d'Ambohipo, *Camboué*, PC. Analamainty, *Campeon*, PC, holotype (N.S.).
- Polytrichum subpilosum* P. Beauv. (Crosby *et al.*, 1983; De Sloover, 1986)
- Pottiaceae**
- Anoetangium impressum* Hampe (Crosby *et al.*, 1983)
- Anoetangium madagassum* Renauld *et* Paris (Crosby *et al.*, 1983) **End**, Type – Pays des Betsileo, *Villaume*, herb (N.S.).
- Anoetangium rufoviride* Besch. (Crosby *et al.*, 1983)
- Barbula bolleana* (Müll.Hal.) Broth. (Crosby *et al.*, 1983)
- Barbula eubryum* Müll.Hal. (O'Shea *et al.*, 1997)
- Barbula indica* (Hook.) Spreng. var. *indica* (Crosby *et al.*, 1983)
- Barbula jananicus* O'Shea (O'Shea, 2008) **End**, Type – Janjanina, carton de Mahaiza, herb (N.S.).
- Barbula omissa* Thér. (Sim & Dixon, 1922)
- Barbula subobtusa* Thér. (Crosby *et al.*, 1983) **End**, Type – Vondrozo, forêt sur rocher humide au bord d'une cascade, 11/09/1924, *Decary*, holotype PC.
- Bryoerythrophyllum campylocarpum* (Müll.Hal.) H. A. Crum (Sollman, 2009)

- Chionoloma bombayense* (Müll.Hal.) P. Sollm. (Crosby *et al.*, 1983)
- Didymodon subrevolutus* (Hampe) Broth. (Crosby *et al.*, 1983) **End**, Type – 1869, Borgen, holotype PC.
- Gymnostomiella tuberculosa* (Renauld et Paris) Arts et P. Sollm. (Crosby *et al.*, 1983)
- Gymnostomum madagascariense* O’Shea (O’Shea, 2008) **End**, Type – Desvaux, herb (N.S.).
- Hymenostylium subcrispulum* Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, forêt à sous bois herbacé, alt. 1200-2400 m, 04/1924, *Perrier de la Bathie*, holotype PC#
- Hyophila acuminata* Broth. et P. de la Varde (Crosby *et al.*, 1983)
- Hyophila angustifolia* Paris et Renauld (Crosby *et al.*, 1983) **End**, Type – Rive de la Mania, 08/1901, *Galinson*, holotype PC.
- Hyophila involuta* (Hook.) A. Jaeger (Crosby *et al.*, 1983)
- Hyophila lanceolata* Renauld et Cardot (Crosby *et al.*, 1983)
- Hyophila parietalis* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone des savanes occidentales, Marovoay, *Mathieu*, herb (N.S.).
- Hyophila potieri* var. *atroviridis* Renauld et Cardot (Crosby *et al.*, 1983) **End**, Type – Plateau central, Ambohibeloma, Imerina, *Camboué*, holotype PC#
- Hyophila sakalavensis* Paris et Renauld (Crosby *et al.*, 1983)
- Leptodontium flexifolium* (With.) Hampe (Sollman, 2006)
- Leptodontium pungens* (Mitt.) Kindb. (De Sloover, 1987)
- Leptodontium viticulosoides* (P. Beauv.) Wijk et Margad. var. *viticulosoides* (Zander, 1972; Crosby *et al.*, 1983; De Sloover, 1987; Delgadillo, 1995)
- Splachnobryum gracile* Besch. (Crosby *et al.*, 1983)
- Splachnobryum obtusum* (Brid.) Müll.Hal. (Crosby *et al.*, 1983; Arts, 1996; Arts, 2001)
- Streptopogon calymperes* Müll.Hal. ex Geh. (Crosby *et al.*, 1983)
- Streptopogon erythrodontus* (Taylor) Wilson (Crosby *et al.*, 1983; Delgadillo, 1995)
- Tortella humilis* (Hedw.) Jenn. (Crosby *et al.*, 1983)
- Tortula madagassa* Dixon (Crosby *et al.*, 1983) **End**, Type – unknown.
- Tortula muralis* var. *madagascariensis* Thér. (Crosby *et al.*, 1983) **End**, Type – Andrahomana, sur rocher gréseux, *Decary*, herb (N.S.).
- Tortula omissa* Thér. (Crosby *et al.*, 1983) **End**, Type – Imerimandroso, sur écorce, associé à *Bryum truncorum* Brid. *Decary*, holotype PC.
- Tortula subrufa* Cardot (Crosby *et al.*, 1983) **End**, Type – Fianarantsoa, 1905, *Villaume s.n.*, holotype PC, isotype PC.
- Trichostomum brachydontium* Bruch var. *brachydontium* (Crosby *et al.*, 1983)
- Trichostomum pennequinii* Renauld et Paris (Crosby *et al.*, 1983) **End**, Type – Cercle des Bara, secteur d’Ivondro, 1900, *Lespagnol et Croll*, holotype PC.
- Trichostomum perrieri* Thér. (Crosby *et al.*, 1983) **End**, Type – Massif granitique de l’Andringitra, alt. 1600 m, 1921, *Perrier de la Bathie*, holotype PC.
- Trichostomum sporophyllum* (Renauld et Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Ambohibeloma, 1906, *Camboué*, holotype PC.
- Trichostomum tenuirostre* (Hook. et Taylor) Lindb. var. *tenuirostre* (Crosby *et al.*, 1983)

Trichostomum villaumei Thér. (Crosby *et al.*, 1983) **End**, Type – Fianarantsoa, 1905, *Villaume*, holotype PC.

Weisiopsis plicata (Mitt.) Broth. (Crosby *et al.*, 1983)

Weissia ayresii Schimp. (Crosby *et al.*, 1983)

Prionodontaceae

Prionodon ciliatus Besch. (Crosby *et al.*, 1983)

Pterobryaceae

Calyptothecium bescherellei (Renauld) Broth. (Crosby *et al.*, 1983) **End**, Type – Mont Ankaratra, *Borgen*, holotype BM!

Calyptothecium planifrons (Renauld et Paris) Argent (Argent, 1973; Crosby *et al.*, 1983; Delgadillo, 1995)

Hildebrandtiella endotrichelloides Müll.Hal. (Crosby *et al.*, 1983)

Hildebrandtiella longiseta Renauld et Cardot (Crosby *et al.*, 1983) **End**, Type – Diégo-Suarez, 1890, *Chénagon*, holotype PC.

Hildebrandtiella rotundifolia Renauld (Crosby *et al.*, 1983)

Jaegerina solitaria var. *nossi-beana* Besch. (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Nosy Be, *Pervillé*, herb (N.S.).

Jaegerina stolonifera (Müll.Hal.) Müll.Hal. subsp. *stolonifera* (Argent, 1973; Crosby *et al.*, 1983)

Orthostichidium involutifolium (Mitt.) Broth. subsp. *involutifolium* (Crosby *et al.*, 1983)

Orthostichopsis longinervis (Renauld et Cardot) Broth. (Crosby *et al.*, 1983)

Orthostichopsis madagassa Dixon (Crosby *et al.*, 1983) **End**, Type – unknown.

Orthostichopsis scaberula (Renauld et Cardot) M. Fleisch (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, entre Vinanitelo et Ikongo, sur les rameaux grêles des arbres, 1892, *Besson*, holotype PC#

Orthostichopsis subimbricata (Hampe) Broth. (Argent, 1973; Crosby *et al.*, 1983)

Orthostichopsis subimbricata var. *flageyi* (Renauld et Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Diégo-Suarez, *Chénagon*; Zone supérieure, Andrangoloaka, *Sikora*, herb (N.S.).

Pterobryopsis longissima Dixon (Crosby *et al.*, 1983) **End**, Type – unknown.

Renauldia hildebrandtielloides Müll.Hal. (Argent, 1973; Crosby *et al.*, 1983)

Renauldia patentissima (Hampe) Broth. (Argent, 1973; Crosby *et al.*, 1983) **End**, Type – 1892, *Besson*, holotype PC.

Renauldia patentissima var. *mutica* Thér. (Crosby *et al.*, 1983) **End**, Type – Montagne d'Ambre, alt. 1000 m, 9/1926, *Perrier de la Bathie*, holotype PC.

Pterygynandraceae

Trachyphyllum borgenii (Renauld et Cardot) Broth. (Buck, 1979; Crosby *et al.*, 1983; O'Shea, 1999) **End**, Type – Mont Ankaratra, lectotype BM, isolectotypes H, NY

Trachyphyllum inflexum (Harv.) A. Gepp (Buck, 1979; Crosby *et al.*, 1983)

Ptychomitriaceae

Ptychomitrium crispatum (Hedw.) A. Jaeger (Crosby *et al.*, 1983)

Ptychomitrium deltorii (Thér.) Broth. (Crosby *et al.*, 1983)

Pylaisiadelphaceae

- Isopterygium ambreanum* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Diégo-Suarez, sur les écorces, 1890, *Chénagon*, holotype PC.
- Isopterygium antsihanakense* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, pays d'Antsihanaka, *Perrot*, herb (N.S.).
- Isopterygium argillicola* (Renauld *et* Cardot) Broth. (Crosby *et al.*, 1983) **End**, Type – Entre Tananarive et Betafo, *Caussègue*, holotype PC.
- Isopterygium argyroleucum* Besch. (Crosby *et al.*, 1983)
- Isopterygium austrodenticulatum* (Renauld *et* Cardot) Broth. (Crosby *et al.*, 1983) **End**, Type – Andriba, 1897, *Dorr*, holotype PC.
- Isopterygium combae* Besch. (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Nosy Be et Nosy Komba, *Marie*, herb (N.S.).
- Isopterygium gracile* Renauld *et* Cardot (Crosby *et al.*, 1983)
- Isopterygium intortum* (P. Beauv.) A. Jaeger (Crosby *et al.*, 1983)
- Isopterygium intortum* var. *chenagonii* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Diégo-Suarez, *Chénagon*, herb (N.S.).
- Isopterygium leptoblastum* (Müll.Hal.) A. Jaeger (Crosby *et al.*, 1983)
- Isopterygium luteonitens* (Paris) Paris (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, bords gramineux du lac d'Ambohipo, *Camboué*, herb (N.S.).
- Isopterygium meylanii* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Imerina, *Villaume*, holotype G.
- Isopterygium podorrhizum* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Ambatomanga, dans un gazon d'*Éctropothecium regulare*, alt. 1200-1300 m, 1894, *Talazac*, herb (N.S.).
- Isopterygium subleptoblastum* Müll.Hal. (Crosby *et al.*, 1983)
- Taxithelium argyrophyllum* Renauld *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, sur les troncs pourrissants à Diégo-Suarez, *Chénagon*, holotype PC.
- Taxithelium confusum* Cardot (Crosby *et al.*, 1983) **End**, Type – Ile Sainte Marie, *Boivin*, herb (N.S.).
- Taxithelium glaucophyllum* Besch. (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Nosy Be, forêt de Lokobe, *Marie*, herb (N.S.).
- Taxithelium hirtellum* Paris *et* Renauld (Crosby *et al.*, 1983) **End**, Type – Zone des savanes orientales, Maintirano, *Paris 66*, holotype PC.
- **Taxithelium nepalense* (Schwägr.) Broth. – Forêt d'Ankara, Sambirano, sur sol, sur calcaire, alt. 200 m, 21/08/1977, *Tixier 10746*, TAN.
- Taxithelium nossianum* Besch. (Crosby *et al.*, 1983)
- Taxithelium planulum* Besch. (Crosby *et al.*, 1983)
- Wijkia bessonii* (Renauld *et* Cardot) H.A. Crum (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, plateau d'Ikongo, *Besson*, herb (N.S.).
- Wijkia madagassa* (Thér.) H.A. Crum (Crosby *et al.*, 1983) **End**, Type – Vallée de l'Anony, sous-bois, 05/08/1921, *Decary*, holotyp PC.
- Wijkia rutenbergii* (Müll.Hal.) H.A. Crum (Crosby *et al.*, 1983) **End**, Type – Massif d'Ankaizina, herb (N.S.).
- Wijkia rutenbergii* var. *eflagellaris* (Cardot) H.A. Crum (Crosby *et al.*, 1983)

Racopilaceae

Powellia elliptica (Renauld) Zanten (Crosby *et al.*, 1983; Zanten, 2003) **End**, Type – Entre Fianarantsoa et Mananjary, 1880, *Besson*, holotype PC.

Powellia pocsii Zanten (Zanten, 2003)

Racopilum africanum Mitt. (Crosby *et al.*, 1983)

Racopilum cardotii Renauld (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, Diégo-Suarez, 1890, *Chénagon*, PC; Andevoranto, 1896, *Perrot*, PC; holotype (N.S.).

Racopilum madagassum Renauld (Crosby *et al.*, 1983)

Racopilum madagassum var. *grandistipulaceum* Thér. et Renauld (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, pays Betsileo, *Villaume*, holotype BM#

Racopilum marginatum Dixon (Crosby *et al.*, 1983)

Racopilum mauritianum Müll.Hal. ex Besch. (Crosby *et al.*, 1983)

Racopilum microdictyon Besch. (Crosby *et al.*, 1983)

Racopilum perrieri Thér. (Crosby *et al.*, 1983) **End**, Type – Entre la Sahambana et l'Ihosy, Forêt d'Analamanara, alt. 1300 m, 06/1919, *Perrier de la Bathie*, holotype PC.

Racopilum plicatum Renauld et Cardot (Crosby *et al.*, 1983)

Racopilum tomentosum (Hedw.) Brid. (Crosby *et al.*, 1983)

Regmatodontaceae

Regmatodon orthostegius Mont. (Crosby *et al.*, 1983; Eakin, 1998)

Rhabdoweisiaceae

Oreoweisia erosa (Müll.Hal.) Kindb. (Crosby *et al.*, 1983)

Rhachithecaceae

Rhachithecium perpusillum (Thwaites et Mitt.) Broth. (Crosby *et al.*, 1983)

Rhacocarpaceae

Rhacocarpus purpurascens (Brid.) Paris (Crosby *et al.*, 1983; Frahm, 1996; Delgadillo, 1995)

Rhizogoniaceae

Pyrrhobryum spiniforme (Hedw.) Mitt. (Crosby *et al.*, 1983; Frahm *et al.*, 2003; Delgadillo, 1995)

Rigodiaceae

Rigodium toxarion (Schwaegr.) A. Jaeger var. *toxarion* (Crosby *et al.*, 1983; Zomlefer, 1993)

Rutenbergiaceae

Rutenbergia borbonica Besch. (Crosby *et al.*, 1983)

Rutenbergia cirrata Renauld et Cardot (Crosby *et al.*, 1983) **End**, Type – Forêt d'Analamazoatra, *Camboué 295*, holotype PC.

Rutenbergia limbata (Hampe) Besch. (Crosby *et al.*, 1983) **End**, Type – Forêt d'Analamazoatra, *Borchgrevink*, herb (N.S.).

Rutenbergia madagassa Geh. et Hampe (Crosby *et al.*, 1983) **End**, Type – Ambatondrazaka, herb (N.S.).

Rutenbergia madagassa var. *flagelliformis* Renault *et* Cardot (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Ambohimahatsara près d’Ambositra, 1892, *Berthieu*, holotype PC.

Sematophyllaceae

Acanthorrhynchium papillatum (Harv.) M. Fleisch. (Crosby *et al.*, 1983; Tixier, 1995)

Acroporium depressum Thér. (Crosby *et al.*, 1983) **End**, Type – Mont Tsaratanana, forêt à sous-bois herbacé, alt. 1200-2400 m, *Perrier de la Bathie*, holotype PC.

Acroporium laevifolium (Renauld) Broth. (Crosby *et al.*, 1983) **End**, Type – Ankeramadinika, zone supérieure des forêts, 11/1897, *Dorr*, holotype PC.

Acroporium megasporum (Duby) M. Fleisch. (Crosby *et al.*, 1983)

Acroporium megasporum var. *densum* (Renauld *et* Cardot) Wijk *et* Margad. (Crosby *et al.*, 1983) **End**, Type – Forêt entre Fianarantsoa et Mananjary, 1892, *Benson*, holotype PC.

Acroporium stellatum (Renauld *et* Cardot) Broth. (Crosby *et al.*, 1983) **End**, Type – Zone inférieure des forêts, forêt à l’Est de Mahambo, environ d’Andevorante, au milieu de touffes de *Schlotheimia perroti*, 1890-1896, *Perrot*, holotype PC.

Clastobryophilum bogoricum (Bosch *et* Sande Lac.) M. Fleisch. (Crosby *et al.*, 1983)

Macrohymenium acidodon (Mont.) Dozy *et* Molk. (Eakin, 1976; Crosby *et al.*, 1983; Een, 1997)

Macrohymenium muelleri Dozy *et* Molk. (Eakin, 1976)

Macrohymenium rufum Müll.Hal. (Eakin, 1976)

Macrohymenium strictum Bosch. *et* Sande Lac. (Eakin, 1976)

Meiothecium crassirete (Renauld *et* Cardot) Cardot (Crosby *et al.*, 1983) **End**, Type – holotype PC.

Meiothecium madagascariense (Brid.) Broth. (Crosby *et al.*, 1983; Een, 1997)

Meiothecium undulatum (Renauld *et* Cardot) O’Shea (Crosby *et al.*, 1983) **End**, Type – Zone moyenne des forêts, forêt d’Analamazaotra, *Camboué*, herb (N.S.).

Radulina borbonica (Bel.) W.R. Buck (Crosby *et al.*, 1983)

Rhaphidorrhynchium angustissimum (Geh.) Broth. (Crosby *et al.*, 1983) **End**, Type – Forêt de Vondrozona, *Rutenberg*, herb (N.S.).

Rhaphidorrhynchium cambouei (Renauld *et* Cardot) Broth. (Crosby *et al.*, 1983) **End**, Type – Zone du Plateau central, Ankadivavala, *Campeyron*, herb (N.S.).

Rhaphidorrhynchium rubicaule (Besch.) Broth. (Crosby *et al.*, 1983)

Sematophyllum coppeyi (Cardot) Broth. (Crosby *et al.*, 1983) **End**, Type – Forêt de Manongarivo, 1909, *Drouhard*, holotype PC.

Sematophyllum dixonii (Thér.) O’Shea (Crosby *et al.*, 1983) **End**, Type – Vallée de l’Anony, Imerimandroso, Ambatondrazaka, Amparafaravola, 300 km NE, alt. 600 m, 05/08/1921, *Decary & Waterlot*, holotype PC.

Sematophyllum dubium (Renauld) Broth. (Crosby *et al.*, 1983) **End**, Type – Ankeramadinika, 11/1897, *Dorr*, holotype PC.

Sematophyllum nanopyxis (Geh.) O’Shea (Crosby *et al.*, 1983) **End**, Type – Zone des forêts, forêt de Vondrozona, *Rutenberg*, herb (N.S.).

- Sematophyllum obtusifolium* (Renauld et Cardot) Broth (Crosby et al., 1983)
Sematophyllum rigescens (Cardot) O'Shea (Crosby et al., 1983) **End**, Type – Zone inférieure des forêts, forêt de Fito, district de Tamatave, Perrot, holotype FH#
- Sematophyllum sinuosulum* (Besch.) Broth. (Crosby et al., 1983)
Sematophyllum sinuosulum var. *latifolium* (Cardot) Thér. (Crosby et al., 1983) **End**, Type – Zone du Plateau central, province d'Imamo, Camboué, holotype G#
- Sematophyllum subpinnatum* (Brid.) E. Britton (Crosby et al., 1983)
Sematophyllum subrugifolium Dixon (Crosby et al., 1983) **End**, Type – unknown.
Sematophyllum subscabrellum Renauld et Cardot (Crosby et al., 1983) **End**, Type – Andevoranto, au milieu d'autres mousses, 1895, Perrot, holotype PC.
- Trichosteleum debettei* var. *laevisetum* Cardot (Crosby et al., 1983) **End**, Type – unknown.
Trichosteleum heterophyllum Bizot et Onr. (Crosby et al., 1983) **End**, Type – Nord Maromandia, au Sud de Diégo-Suarez, sur sol caillouteux, au bord d'un marigot permanent, sous forêt, alt. 50 m, 13/08/1973, Cremers 2735, holotype BR, isotypes BR, TAN, PC.
- Trichosteleum leviusculum* Renauld et Cardot (Crosby et al., 1983)
Trichosteleum microdontum (Besch.) Renauld (Crosby et al., 1983)
Trichosteleum microdontum var. *megapterum* Renauld et Cardot (Crosby et al., 1983) **End**, Type – Zone moyenne des forêts, forêt d'Analamazaotra, Camboué & Campenon, herb (N.S.).
Trichosteleum permixtum Cardot (Crosby et al., 1983) **End**, Type – Diégo-Suarez, Chénagon, holotype PC.
Trichosteleum perrotii (Renauld et Cardot) Renauld et Cardot (Crosby et al., 1983)
Trichosteleum perrotii var. *eurydictyon* Renauld et Cardot (Crosby et al., 1983) **End**, Type – Zone inférieure des forêts, île de Sainte-Marie, Mahavelona ou Foulpointe, Darbould, herb (N.S.).
Trichosteleum pervilleanum (Müll.Hal. ex Geh.) W.R. Buck (Crosby et al., 1983)
Trichosteleum trachypyxis (Geh.) Renauld et Cardot (Crosby et al., 1983) **End**, Type – Zone moyenne des forêts, forêt à l'est d'Ambatondrazaka, Rutenberg, herb (N.S.).
Warburgiella leptorrhyncha (A. Jaeger) Broth. (Crosby et al., 1983)
- Serpotortellaceae**
Serpotortella chenagonii (Renauld et Cardot) W.D. Reese et R.H. Zander (Crosby et al., 1983)
Serpotortella cyrtophylla (Besch.) W.D. Reese et R.H. Zander (Reese & Zander, 1987)
- Sphagnaceae**
Sphagnum capense Hornsch. (Eddy, 1985)
Sphagnum ceylonicum Mitt. ex Warnst. (Eddy, 1985)
Sphagnum cuspidatum Müll.Hal. (Eddy, 1985)
Sphagnum cuspidatum Hoffm. var. *cuspidatum* (Eddy, 1985)
 **Sphagnum davidii* Warnst. – Massif de l'Ankaratra, S 19°20' E 47°20', alt. 2100 m, 24/10/1972, M.R. & C.A. Crosby 6636, TAN.

- Sphagnum ericetorum* Brid. (Eddy, 1985)
Sphagnum magellanicum (Warnst.) A. Eddy subsp. *grandirete* (Eddy, 1985) **End**,
 Type – Andevoranto, Androrangobe, 1901, holotype PC.
Sphagnum perichaetiale Hampe (Eddy, 1985)
Sphagnum perrieri Thér. (Crosby *et al.*, 1983) **End**, Type – Massif de l'Andringitra,
 alt. 1600-2500 m, 1921, *Perrier de la Bathie*, holotype PC.
Sphagnum planifolium var. *angustilimbatum* (Warnst.) A. Eddy (Eddy, 1985)
Sphagnum planifolium Müll.Hal. var. *planifolium* (Eddy, 1985)
Sphagnum rutenbergii Müll.Hal. (Eddy, 1985)
Sphagnum strictum (Müll.Hal.) A. Eddy subsp. *pappeanum* (Eddy, 1985)
Sphagnum truncatum var. *bordasii* (Besch.) A. Eddy (Eddy, 1985)
Sphagnum tumidulum Besch. var. *tumidulum* (Eddy, 1985)
Sphagnum violascens Müll.Hal. (Eddy, 1985)
- Splachnaceae**
Brachymitrium moritzianum (Müll.Hal.) A.K. Kop. (Koponen & Weber, 1972;
 Crosby *et al.*, 1983)
Tayloria indica Mitt. (Crosby *et al.*, 1983)
Tayloria isleana (Besch.) Broth. (Crosby *et al.*, 1983)
Tayloria orthodonta (P.Beauv.) Wijk *et* Margad. (Crosby *et al.*, 1983; Pócs &
 Geissler, 2002)
Tayloria solitaria (Hedw.) T.J. Kop *et* W. Weber (Crosby *et al.*, 1983; Pócs &
 Geissler, 2002)
- Stereophyllaceae**
Entodontopsis nitens (Mitt.) W.R. Buck *et* Ireland (Crosby *et al.*, 1983)
Entodontopsis tenuinervis (Broth.) W.R. Buck *et* Ireland (Crosby *et al.*, 1983)
Stereophyllum radiculosum (Hook.) Mitt. (Crosby *et al.*, 1983)
- Symphyodontaceae**
Symphyodon pygmaeus (Broth.) S. He *et* Snider (Crosby *et al.*, 1983; He & Snider,
 2000)
- Thuidiaceae**
Pelekium chenagonii (Müll.Hal. *ex* Renaud *et* Cardot) Touw (Touw, 1976; Crosby
et al., 1983)
Pelekium gratum (P. Beauv.) Touw (Touw, 1976; Crosby *et al.*, 1983; Touw, 2001)
Pelekium intricatum (A. Jaeger) Touw (Pócs & Geissler, 2002)
Pelekium investe (Mitt.) Touw (Touw, 1976; Crosby *et al.*, 1983; Touw, 2001; Pócs
 & Geissler, 2002)
Pelekium ramusculosum (Mitt.) Touw (Touw, 1976; Crosby *et al.*, 1983)
Pelekium varians (Welw. *et* Duby) Touw (Touw, 1976; Crosby *et al.*, 1983)
Pelekium versicolor (Müll.Hal.) Touw (Touw, 1976; Crosby *et al.*, 1983; Touw,
 2001)
Rauarella praelonga (Schimp. *ex* Besch.) Wijk *et* Margad. (Touw, 1976; Crosby *et*
al., 1983)
Thuidium aculeoserratum Renaud *et* Cardot (Touw, 1976; Crosby *et al.*, 1983)
Thuidium assimile (Mitt.) A. Jaeger (Touw, 1976; Crosby *et al.*, 1983)
Thuidium pseudoinvolvens (Müll.Hal.) A. Jaeger (Touw, 1976; Crosby *et al.*, 1983)

Note on *Riccardia*:

According to Grolle 1995, three species of the genus *Aneura*: *A. caespitans* Steph., *A. corbieri* Steph and *A. dismieri* Steph. were placed on the name of *Riccardia* sp. The attribution of those species to the genus *Riccardia* has not been revised. But since the revision of the genus *Riccardia* from Africa and Madagascar is now in a progress, most of the morphological and reproductive characters of those three species seem to fit with those of *Riccardia*. We decided to keep the name used by Grolle (1995) and Wigginton (2009).

CONCLUSION

In total 1144 bryophyte species and infraspecific taxa, including 751 mosses, 390 liverworts and 3 hornworts are reported from Madagascar (Table 1). The following families: Dicranaceae (83 species and infraspecific taxa), Orthotrichaceae (66 species and infraspecific taxa) and Bryaceae (44 species and infraspecific taxa) are the most speciose for mosses and the Lejeuneaceae (203 species and infraspecific taxa), Frullaniaceae (38 species and infraspecific taxa) and Plagiochilaceae (21 species and infraspecific taxa) for liverworts. The lack of reported hornwort taxa undoubtedly represents a significant bias in historic collecting effort especially since more than 5 hornwort taxa are reported for Réunion Island, a landmass both a fraction of the age and size of Madagascar (Ah-Peng *et al.*, 2010). Future floristic exploration in Madagascar should target such little known groups as they are likely to harbour a wealth of unknown diversity.

In this checklist, 13 mosses, 10 liverworts and one species of hornwort are newly recorded for Madagascar. The majority of these new records are reported from collections in the National Herbarium of Madagascar (TAN) and from recent collections by the authors. Two species: *Fissidens cyathaeicola* Brugg.Nann. and *Taxithelium nepalense* (Schwägr.) Broth. are reported for the first time for the Sub-Saharan Africa region.

The bryoflora of Madagascar displays remarkably high levels of endemism, 33.82% of mosses and 18.97% of liverworts are unique to the island, providing ample support for its status as a global hotspot of biodiversity. The moss

Table 1. Summary of the bryoflora of Madagascar

	<i>Mosses</i>	<i>Liverworts</i>	<i>Hornworts</i>	<i>Total</i>
Taxa	751	390	3	1144
Genera	186	86	3	275
Families	59	30	2	91
Endemics	254	74	0	328
Endemicity (%)	33.82%	18.97%		28.67%

families with the largest number of endemic species are the Dicranaceae (41/83), Orthotrichaceae (38/66) and Sematophyllaceae (22/40). Of the 74 endemic liverwort species recorded on the island, 59 belong to the family Lejeuneaceae, of which the most important is the epiphyllous genus *Cololejeunea* which has radiated throughout Madagascar and the neighbouring islands (Pócs, 1997). The number of endemics should be regarded with caution as many of the species were described a long time ago and have yet to form part of a recent revision: this figure will need to be continuously updated.

To help in further research e.g. taxonomic revision, we listed the type specimens of endemic species including specimen information and host herbarium. Unfortunately a few proportion (18) of type specimens are poorly detailed, often providing only "Madagascar" as the type location, we did not manage to identify the host herbarium of 56 endemic species.

Since much of the original bryological exploration of Madagascar took place during the late 1800's (Dorr, 1997) it is not known what proportion, if any, of the recorded taxa have been lost due to anthropogenic destruction of habitats for farming and logging. Many of the sites which were frequented by early bryologists have been lost due to such activities. New inventories of intact and unexplored habitats on the island should prove invaluable for verifying many of the old records presented in this checklist and will undoubtedly reveal many new and interesting records for the island.

Much work remains to be done to improve knowledge on the diversity and distribution of bryophytes in Madagascar. For example, collections of bryophytes in the National Herbarium of Madagascar (TAN) need to be revised and fully identified. More fieldwork to collect bryophytes in poorly investigated areas should be planned, especially in areas such as the dry forests.

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Appendix 2: A collection of mosses and liverworts in Marojejy National Park, North-eastern Madagascar

A collection of mosses and liverworts collected in Marojejy National Park, North-eastern Madagascar

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Abstract – New and remarkable records of epiphytic bryophytes from Marojejy National Park, Northern Madagascar are presented in this paper. As a result of a bryological expedition in 2009, 255 species of bryophytes belonging to 92 genera and 39 family (158 liverworts and 97 mosses) are reported. 8.92% of those species are endemics of Madagascar and 39 taxa are newly recorded for the Island.

Key words: bryophytes, diversity, tropical mountain, rainforest, Madagascar

INTRODUCTION

The Marojejy National Park located in the Sava Region, north-eastern Madagascar, covers 55,500 ha of land, and protects the entire massif of the same name. From the Indian Ocean, the escarpment of the mountain reaches quickly an altitude of 2132 m because of very high slopes. The wide range of elevations and rugged topography of the massif create diverse habitats that transition quickly with changes in altitude. Ninety percent of the National Park is covered in forests which are unevenly distributed and extremely varied. At low altitude (below 800 m) an evergreen Rainforest occurs sheltered from strong winds and stimulated by consistently warm temperatures together with abundant rainfall. In disturbed areas, secondary growth consists primarily of bamboo, wild ginger and ravinala. A medium-altitude Rainforest occurs at 800-1400 m, with cooler temperatures and increasingly impoverished soils supporting increasingly smaller trees and shrubs. A high altitude montane cloud forest occurs at 1400-1800 m, with lower temperatures further reducing forest growth (Goodman 2000). Winds from the east envelope the higher forest in heavy cloud cover. The trees are short, gnarled and stunted, and mosses and lichens drape their branches. A high altitude Montane Scrub occurs above 1800 m, with cool, windy conditions, lower rainfall, and thin rocky soils limiting the vegetation to dense thickets of shrubs, which form an open, tundra-like cover, with miniature palms and bamboos, as well as terrestrial orchids. This is the only montane scrub left intact in Madagascar; the vegetation on all other high mountain peaks has been destroyed by fire (Goodman 2000; Garreau & Manantsara 2003;).

Marojejy National Park is one of the highest peak of Madagascar that has always fascinated scientists and non-scientists. Its flora and fauna have been studied by many biologists but only very few collections of bryophytes are made. A study of the structure of bryophyte assemblages along an elevational gradient was conducted in Marojejy National Park in November 2009, with the participation of eight bryologists from Madagascar (Andriamiarisoa Lala Roger & Lova Marline), South Africa (Terry Hedderson & Nicholas Wilding), Malaysia (Min Chuah-Petiot), and France (Jacques Bardat & Claudine Ah-Peng). This study is part of a multidisciplinary and transnational body of research on a comparative survey of bryophytes and fern along an elevational gradient across Islands in the Indian Ocean region (BRYOLAT).

Since the publication of the first checklist of the bryophytes of Madagascar (Marline *et al.*, 2012), citing more than thousand species of bryophytes and 32% of

endemism, changes have been made in the nomenclature of different families and new species have been discovered. In the present study, we sought a taxonomic inventory of the epiphytic bryophytes in Marojejy National Park of epiphytic bryophyte. We have only focused on the epiphytic bryophytes since they are important components of tropical forests, especially the mountain areas, and might play a significant role in ecosystem services, namely water balance and nutrient cycling of such type of forests.

This paper provides a list of epiphytic bryophytes species collected along an elevational transect in Marojejy National Park.

METHODS

Sampling method

Bryophytes samples were collected in November 2009 by a multinational group of bryologists. Bryophytes were collected along an elevational transect at 200 m intervals from 250 m to 2050 m (10 sites in total) using a hierarchically nested design. Sampling was undertaken at four hierarchical levels: elevational belt, plots, quadrats and microhabitat. The epiphytic microhabitat is composed of TA (0- 0.5 m), TB (0.5-1 m) and TC (1-2 m), the canopy for practical reasons was not investigated in this study (Ah-Peng *et al.*, 2007; Ah-Peng *et al.*, 2012; Gabriel *et al.*, 2014). In the field, samples of bryophytes were air-dried. Species identification was performed with a binocular and a compound microscope in the laboratory. Since there is no available key for the bryophytes of Madagascar, available literature and herbarium collections were used as references.

Format of the list

Synopses of family are based on the work of Crandall-Stotler *et al.*, (2009) for liverworts and Goffinet *et al.*, (2009) for mosses. Species nomenclature follows Marline *et al.*, (2012) with recent taxonomical modifications for Liverworts from Söderström *et al.*, (2016) world checklist of hornworts and liverworts. Taxa are arranged alphabetically within Marchantiophyta (liverworts) and Bryophyta (mosses) and within each family. Endemic taxa are followed by “**End**”. New addition to bryoflora of Madagascar are preceded by *. The elevational ranges of each species are presented in bracket after the scientific name. Ecological samples are stored in bolus herbarium.

RESULTS AND DISCUSSIONS

From the ecological samples, a total of 457 epiphytic bryophyte samples of 50 cm² were collected along the elevational transect in the Marojejy National Park, yielding

2454 identifications of species. Bryophytes richness ranges from 1 to 30 species per microplot of 50 cm².

A total 255 species of bryophytes, including 97 moss species and 158 liverworts species, belonging to 92 genera and 39 family are reported for Marojejy National Park. Twenty-three species, representing 8.92% of the epiphytic bryophytes collected along the transect are endemic to Madagascar. Endemic species are mostly represented by members of the moss family Dicranaceae (9 endemic species) and liverwort family Lejeuneaceae (7 endemic species).

The genera with the highest number of species for mosses in this study were Dicranaceae (29 species), Orthotricaceae (16 species), Sematophyllaceae (13 species) and Calymperaceae (11 species). Lejeuneaceae (73 species), Lepidoziaceae (19 species), Frullaniaceae (15 species) and Plagiochilaceae (11 species) were the richest genera in terms of species number within the liverworts.

Thirty-nine new species were added to the bryoflora of Madagascar. Fifty percent of new additions belong to the family of Lejeuneaceae, 20% belong to the family of Lepidoziaceae and and 13% to the family of Plagiochilaceae. The rest, representing 15% of the new additions belong to the Frullaniaceae, Lophocoleaceae, Metzgeriaceae, Scapaniaceae and Cephaloziaceae families.

Liverworts reported for Marojejy National Park

Adelanthaceae

Adelanthus decipiens (Hook.) Mitt. (alt 1050-1650 m)

Adelanthus lindenbergianus (Lehm.) Mitt. (alt 150-1650 m)

Anastrophyllaceae

**Anastrophyllum auritum* (Lehm.) Steph. (alt 1250-1850 m)

Anastrophyllum piligerum (Nees) Steph. (alt 1250-2050 m)

Aneuraceae

Riccardia longispica (Steph.) Pearson (alt 1650 m)

Riccardia nudiflora (Steph.) Grolle (alt 1050-1650 m)

Balantiopsidaceae

Isotachis aubertii (Schwaegr.) Mitt. (alt 1250 m)

Calypogeiaceae

Calypogeia fissa (L.) Raddi. (alt 1050 m)

Mnioloma fuscum (Lehm.) R.M. Schust. (alt 1250-1850 m)

Cephaloziaceae

Cephalozia connivens ssp. *fissa* Váná (alt 850-1050 m)

Iwatsukia jishibae (Steph.) N. Kitag. (alt 1250 m)

Cephaloziellaceae

Cephaloziella kiaeri (Austin) S.W. Arnell (alt 1250-1450 m)

**Cephaloziella vaginans* Steph. (alt 1250-1450 m)

Frullaniaceae

Frullania anderssonii Aongstr. (alt 250-850)

Frullania angulata Mitt. (alt 1250 m)

Frullania apicalis Mitt. (alt 1050-1850 m)

Frullania apiculata (Reinw. Blume & Nees) (alt 850-2050 m)

Frullania capensis Gottsche (alt 850 m)

**Frullania eplicata* Stephani (alt 1250-2050 m)

Frullania gabonensis Vanden Berghen (alt 850-1050 m)

Frullania grossiclava Steph. (alt 1850 m)

Frullania humbertii Vanden Berghen (alt 1250-1850 m)

**Frullania letestui* (alt 1250 m)

Frullania lindenbergii Lehm. (alt 850-1850 m)

Frullania purpurea Steph. (alt 250 m)

Frullania serrata Gottsche (alt 1250-1450 m)

Frullania vanden-berghenii Pócs (alt 1250 m)

Frullania variegata Steph. (alt 1050 m)

Herbertaceae

Herbertus dicranus (Taylor ex Gottsche et al.) Trevis. (alt 1250-2050 m)

Herbertus juniperoideus (Sw.) Grolle (alt 1250-2050 m)

Jamesoniellaceae

Syzygiella geminifolia (Mitt.) Steph. (alt 1250-1650 m)

Lejeuneaceae

- Acanthocoleus madagascariensis* (Steph.) Kruijt (alt 1050 m)
Acrolejeunea pycnoclada (Taylor) Schiffn. (alt 1250 m)
**Archilejeunea linguifolia* Steph. (alt 450 m)
Caudalejeunea lewallei Vanden BergheN (alt 1250 m)
Ceratolejeunea belangeriana (Gottsche) Steph. (alt 250-1250 m)
Ceratolejeunea calabariensis Steph. (alt 250-1050 m)
Ceratolejeunea cornuta (Lindenb.) Schiffn. (alt 1050 m)
**Ceratolejeunea diversicornua* Steph. (alt 650 m)
**Ceratolejeunea floribunda* Stephani (alt 1050 m)
Ceratolejeunea papuliflora Steph. (alt 450 m)
**Ceratolejeunea stictophylla* Herzog ex Vanden Berghen (alt 250-1050 m)
Ceratolejeunea variabilis (Lindenb.) Pearson (alt 1050-1250 m)
Cheilolejeunea cordistipula (Steph.) Grolle ex E.W. Jones (alt 250-1850 m)
Cheilolejeunea decursiva (Sande Lac.) R.M. Schust. (alt 250 m)
Cheilolejeunea intertexta (Lindenb.) Steph. (alt 250-850 m)
Cheilolejeunea krakakammae (Lindenb.) R.M. Schust. (alt 1250-1850 m)
Cheilolejeunea montagnei (Gottsche) R.M. Schust. (alt 1050-2050 m)
Cheilolejeunea serpentina (Mitt.) Mizut. (alt 850-1250 m)
Cheilolejeunea surrepens (Mitt.) E.W. Jones (alt 250-1250 m)
Cheilolejeunea trifaria (Reinw., Blume & Nees) Mizut. (alt 450-1850 m)
Cheilolejeunea usambarana (Steph.) Grolle (alt 850-1050 m)
Cololejeunea andapania Tixier **End** (alt 450 m)
Cololejeunea androphylla var. *madecassa* Tixier **End** (alt 850 m)
Cololejeunea appressa (A. Evans) Benedix (alt 250-1050 m)
Cololejeunea duvignaudii E.W. Jones (alt 450-650 m)
Cololejeunea elegans Steph. (alt 450 m)
Cololejeunea floccosa (Lehm. & Lindenb.) Schiffn. (alt 650 m)
**Cololejeunea haskarliana* (Lehm. et Lindenb.) Schiffn. (alt 250-850 m)
Cololejeunea lemuriana Tixier (alt 250 m)
**Cololejeunea peponiformis* Mizut. (alt 850-1250 m)
Diplasiolejeunea cornuta Steph. (alt 1450 m)
Diplasiolejeunea ensifera Tixier **End** (alt 2050 m)

Drepanolejeunea cambouena Steph. (alt 1650 m)
Drepanolejeunea cultrella (Mitt.) Steph. (alt 1650-2050 m)
Drepanolejeunea madagascariensis (Steph.) Grolle (alt 1650 m)
Drepanolejeunea mascarena (S.W. Arnell) R.L. Zhu et Grolle (alt 1250 m)
Drepanolejeunea physaefolia (Gottsche) Steph. (alt 850-2050 m)
 **Drepanolejeunea vandenberghenii* Buchbender & Eb. Fisch (alt 1250 m)
Lejeunea anisophylla Mont (alt 850 m)
Lejeunea caespitose Lindenb. (alt 250-850 m)
Lejeunea confusa E.W.Jones (alt 250-1050 m)
Lejeunea eckloniana Lindenb. (alt 250-1250 m)
Lejeunea flava (Sw.) Nees (alt 250-1650 m)
 **Lejeunea helenae* Pearson (alt 850 m)
Lejeunea isophylla E.W.Jones (alt 450-1850 m)
 **Lejeunea lomana* E.W.Jones (alt 1450 m)
Lejeunea obtusata Gottsche (alt 1050-1650 m)
 **Lejeunea ramosissima* Steph. (alt 650-1650 m)
Lejeunea tabularis (Spreng.) Gottsche et al. (alt 250-1450 m)
Lejeunea tuberculosa Steph. (alt 450-1250 m)
Lejeunea vojtkoi Pócs **End** (alt 850 m)
 **Leptolejeunea maculata* (Mitt.) Schiffn. (alt 250 m)
Leucolejeunea xanthocarpa (Lehm. et Lindenb.) A.Evans (alt 1850 m)
Lopholejeunea eulopha (Taylor) Schiffn. (alt 850 m)
Lopholejeunea lepidoscypha Kiaer & Pearson **End** (alt 2050 m)
 **Lopholejeunea minima* Vanden Berghen (alt 850 m)
Lopholejeunea multilacera Steph. (alt 250-2050 m)
Lopholejeunea nigricans (Lindenb.) Schiffn. (alt 250-1050 m)
Lopholejeunea onraedtii Vanden Berghen **End** (alt 850-1050 m)
 **Lopholejeunea paramultilacera* Vanden Berghen (alt 250-850 m)
Lopholejeunea quinquecarinata Vanden Berghen (alt 250-850 m)
Lopholejeunea subfusca (Nees) Schiffn. (alt 250-1050 m)
Lopholejeunea tixieriana Vanden Berghen **End** (alt 1050 m)
Mastigolejeunea auriculata (Wilson) Schiffn. (alt 850-1850 m)
Microlejeunea africana Steph. (alt 250-1250 m)
 **Microlejeunea ankasica* E.W.Jones (alt 1050-1650 m)

Microlejeunea inflata Steph. (alt 850 m)
Microlejeunea oblongistipula (Gottsche) Pearson (alt 1250 m)
Prionolejeunea grata (Gottsche) Schiffn. (alt 250-1650 m)
Schiffneriolejeunea pappeana (Nees) Gradst. (alt 1250-1650 m)
Schiffneriolejeunea polycarpa (Nees) Gradst. (alt 650-850 m)
Taxilejeunea conformis (Mont. & Nees) Steph. (alt 650-1050 m)
Thysananthus spathulistipus (Reinw., Blume & Nees) Lindenb. (alt 250-1250 m)

Lepidoziaceae

Amazoopsis diplopoda (Pócs) J.J. Engel & G.L.S. Merr. (alt 650 m)
**Bazzania comorensis* Steph. (alt 1250-1450 m)
Bazzania curvidens Steph. **End** (alt 1050-1250 m)
Bazzania decrescens (Lehm. & Lindenb.) Trevis. (alt 1050-1850 m)
**Bazzania decrescens* subsp. *molleri* (Steph.) E.W.Jones (alt 1050-2050 m)
Bazzania decrescens ssp. *pumila* (Mitt.) Pócs (alt 1050-2050 m)
Bazzania mascarena (Steph.) Herzog (alt 1650 m)
Bazzania nitida (F.Weber) Grolle (alt 250-1650 m)
Bazzania orbanii Pócs **End** (alt 1250-1650 m)
Bazzania praerupta (Reinw., Blume & Nees) Trevis. (alt 1250-2050 m)
**Bazzania roccatii* Gola (alt 850-1250 m)
Kurzia capillaris (Sw.) Grolle (alt 1050-2050 m)
Kurzia capillaris ssp. *stephanii* (Renauld ex Steph.) Pócs (alt 1650-1850 m)
Lepidozia africana Steph. (alt 1650 m)
**Lepidozia stuhlmannii* Steph. (alt 1650 m)
Lepidozia succida Mitt. (alt 850 m)
Telaranea bischleriana Pócs (alt 850-1250 m)
Telaranea coactilis (Spruce) J.J. Engel & G.L.S. Merr. (alt 250-1250 m)
Telaranea nematodes (Gottsche ex Austin) M. Howe (alt 1450 m)

Lophocoleaceae

Chiloscyphus difformis (Nees) J.J. Engel & R.M. Schust. (alt 450 m)
Chiloscyphus muricatus (Lehm.) J.J. Engel & R.M. Schust. (alt 450-1650 m)
Conoscyphus trapezioides (Sande Lac.) Schiffn. (alt 1250-2050 m)
Heteroscyphus dubius (Gottsche) Schiffn. (alt 250-1250 m)

**Heteroscyphus mascarenensis* (alt 1050-2050 m)

**Heteroscyphus spectabilis* (Stephani) Schiffn. (alt 1050-1450 m)

Heteroscyphus splendens (Lehm. & Lindenb.) Grolle (alt 1250-1850 m)

Mastigophoraceae

Mastigophora diclados (Brid. ex F.Weber) Nees (alt 850-2050 m)

Metzgeriaceae

**Metzgeria crassipilis* (Lindb.) A.Evans (alt 250 m)

Metzgeria furcata (L.) Dumort. (alt 450 m)

Metzgeria madagassa Steph. (alt 250 m)

Metzgeria nudifrons Steph. (alt 2050 m)

Plagiochilaceae

Plagiochila angusta Lindenb. (alt 450 m)

Plagiochila barteri Mitt. (alt 1250-1850 m)

**Plagiochila barteri* var. *valida* (Steph.) Vanden Berghen (alt 1250-1650 m)

**Plagiochila fusifera* Taylor (alt 1050 m)

Plagiochila granditexta Steph. **End** (alt 1050 m)

Plagiochila incerta Gottsche (alt 450-850 m)

Plagiochila kiaeri Gottsche (alt 1250 m)

Plagiochila pectinata Willd. ex Lindenb. (alt 1050-2050 m)

**Plagiochila pinniflora* Steph. (alt 850-1250 m)

**Plagiochila renauldii* Steph. (alt 1250 m)

Plagiochila repanda (Schwaegr.) Lindenb. (alt 850-1540 m)

Plagiochila terebrans Nees & Mont. ex Lindenb. (alt 450 m)

Pleuroziaceae

Pleurozia gigantea (F.Weber) Lindb. (alt 1250-1850 m)

Radulaceae

Radula ankefinensis Gottsche ex Steph. (alt 450 m)

Radula appressa Mitt. (alt 650-1050 m)

Radula boryana (F.Weber) Mont. (alt 450 m)

Radula fulvifolia (Hook.f. & Taylor) Gottsche et al. (alt 450-1050 m)

Radula madagascariensis Gottsche (alt 850-1850 m)

Radula stenocalyx Mont. (alt 650-1650 m)

Radula voluta Taylor ex Gottsche et al. (alt 850-1050 m)

Scapaniaceae

Plicanthus hirtellus (F. Weber) R.M. Schust. (alt 1450-1850 m)

Schistochilaceae

Gottschea neesii (Mont.) R.M.Schust. (alt 1650 m)

Mosses reported from Marojejy National Park

Brachytheciaceae

Squamidium brasiliense (Hornsch.) Broth. (alt 1250 m)

Calymperaceae

Calymperes hispidum Renault & Cardot (alt 250-850 m)

Calymperes taitense (Sull.) Mitt. (alt 250-450 m)

**Leucophanes angustifolium* Renault & Cardot (alt 450 m)

Leucophanes hildebrandtii Müll.Hal. (alt 450-850)

Leucophanes renauldii Cardot (alt 250-1450 m)

Leucophanes rodriguezii Müll.Hal. (alt 1050 m)

Syrrhopodon albidus ssp. *integrifolius* (E.B.Bartram) L.T. Ellis (alt 1250 m)

Syrrhopodon gardneri (Hook.) Schwaegr. (alt 1250 m)

Syrrhopodon gaudichaudii Mont. (alt 1250-1450 m)

Syrrhopodon hispidocostatus Renault & Cardot in Renault (alt 850-1650 m)

Syrrhopodon prolifer var. *acanthoneuros* (Müll.Hal.) Müll. Hal. (alt 850-1650 m)

Syrrhopodon prolifer var. *prolifer* Schwaegr. (alt 1250 m)

Dicranaceae

Dicranoloma billardierei (Brid. ex Anon.) Paris (alt 1250-1850 m)

Dicranoloma billardieri var. *scopareolum* (Müll.Hal.) Thér. (alt 1250-1650 m)

Dicranum johnstonii Mitt. (alt 1050-1850 m)

Holomitrium borbonicum Besch. (alt 1450 m)

Holomitrium gracilisetum Thér. **End** (alt 1250)

Leucoloma bifidum (Brid.) Brid. (alt 450-1650m)

Leucoloma boivinianum var. *boivinianum* Besch. (alt 1250 m)

Leucoloma candidum Broth. In Voeltzk. **End** (alt 1250 m)
Leucoloma chrysobasilare var. *chrysobasilare* (Müll.Hal.) A. Jaeger (alt 450-1050 m)
 **Leucoloma cinclidotioides* Besch.(alt 1250 m)
Leucoloma cuneifolium (Hampe ex Müll.Hal. and Geh.) C.H. Wright (alt 1650 m)
Leucoloma dichelymoides (Müll.Hal.) A. Jaeger (alt 650-1850 m)
Leucoloma fontinaloides Dixon **End** (alt 1450-1650 m)
 **Leucoloma gracilescens* Broth. (alt 1250 m)
Leucoloma grimmiioides P. de la Varde (alt 1250-1650)
 **Leucoloma holstii* Broth. (alt 450-1250 m)
Leucoloma lepervancheri Besch. (alt 250-1650 m)
Leucoloma madagascariense La Farge **End** (alt 450-1650 m)
Leucoloma marojeziense La Farge **End** (alt 1450-1650 m)
Leucoloma membranaceum La Farge (alt 1050-1450 m)
Leucoloma ochrobasilare Ren. (alt 450)
Leucoloma rutenbergii (Geh.) C.H. Wright **End** (alt 850-1050 m)
Leucoloma sanctae-mariae Besch. (alt 1450-1650 m)
Leucoloma subchrysobasilare Renauld **End** (alt 1050-1850 m)
Leucoloma thraustum Hampe ex Besch. **End** (alt 250-1850 m)
Leucoloma thuretii Besch. **End** (alt 1850)

Fissidentaceae

Fissidens aristifer Brugg.-Nann. (alt 850 m)
Fissidens asplenioides Hedw. (alt 250 m)
Fissidens punctulatus Sande Lac (alt 450-850 m)
Fissidens serratus var. *serratus* Müll.Hal. (alt 250-450 m)

Hypnaceae

Mittenothamnium reptans (Hedw.) Cardot (alt 850 m)

Hypopterygiaceae

Hypopterygium tamarisci (Sw. ex Sw.) Brid. ex Müll.Hal. (alt 850 m)
Lopidium struthiopteris (Brid.) M. Fleisch. (alt 450-850 m)

Lembophyllaceae

Pilotrichella isleana var. *nervosa* (Renauld & Cardot) Cardot **End** (alt 450 m)

Leucobryaceae

Campylopus arctocarpus ssp. *madecassus* (Besch.) J.-P. Frahm (alt 1450-1850 m)

Campylopus arcuatus (Brid.) A. Jaeger (alt 1650-180 m)

Campylopus flexuosus var. *flexuosus* (Hedw.) Brid. (alt 1650 m)

Campylopus nivalis var. *nivalis* (Brid.) Brid. (alt 1250-1850 m)

**Campylopus robillardei* Besch. (alt 1450 m)

Leucobryum isleanum Besch. (alt 450-650 m)

Leucomiaceae

Leucomium strumosum (Hornsch.) Mitt. (alt 450-650 m)

Meteoriaceae

Aerobryopsis capensis (Müll.Hal.) M. Fleisch. (alt 450-1250 m)

Floribundaria floribunda (Dozy & Molk.) M. Fleisch. (alt 450-650 m)

Trachypodopsis serrulata var. *serrulata* (P. Beauv.) M. Fleisch. (alt 450-1850 m)

Neckeraceae

Homali dendron exiguum (Bosch & Sande Lac.) M. Fleisch. (alt 450-650 m)

Neckeropsis disticha (Hedw.) Kindb. (alt 450-850 m)

Neckeropsis madecassa (Besch.) M. Fleisch. (alt 650 m)

Porotrichum elongatum (Welw. & Duby) A. Gepp (alt 450-850 m)

Porotrichum madagassum Kiaer ex Besch. (alt 450-650 m)

Porotrichum usagarum Mitt. (alt 450-850 m)

Porotrichum variifolioides (De Sloover) Enroth (alt 450 m)

Orthotricaceae

Macromitrium fasciculare Mitt. (alt 1250 m)

Macromitrium fimbriatum (P.Beauv.) Schwaegr. (alt 1450-1850 m)

Macromitrium mauritianum Schwaegr. (alt 1250 m)

Macromitrium serpens (Bruch ex Hook. & Grev.) Brid. (alt 1250 m)

Macromitrium sulcatum var. *sulcatum* (Hook.) Brid. (alt 1250-850 m)

**Schlotheimia angulosa* P.Beauv.(alt 1250-2050 m)

Schlotheimia badiella var. *helicophylla* Besch. (alt 1250-2050 m)

Schlotheimia badiella Besch. (alt 1250-1650 m)

Schlotheimia excorugata Müll.Hal. ex Cardot (alt 1250 m)

**Schlotheimia ferruginea* (Bruch ex Hook. & Grev.) Brid. (alt 1450-2050 m)

Schlotheimia fornicata Duby (alt 1850 m)

Schlotheimia microcarpa Geh. (alt 1450 m)

**Schlotheimia percuspidata* Müll. Hal. (alt 1650-2050 m)

Schlotheimia squarrosa Brid. (alt 1850 m)

Pterobryaceae

Calypothecium planifrons (Renauld & Paris) Argent (alt 850 m)

Orthostichopsis longinervis (Renauld & Cardot) Broth. (alt 450-850 m)

Pylaisiadelphaceae

Isopterygium intortum (P. Beauv.) A. Jaeger (alt 850 m)

Racopilaceae

Racopilum africanum Mitt. (alt 650 m)

Racopilum madagassum Renauld (alt 650-1050 m)

Rhizogoniaceae

Pyrrhobryum spiniforme (Hedw.) Mitt. (alt 450-1050 m)

Rutenbergiaceae

Rutenbergia limbata (Hampe) Besch. **End** (alt 850-1650 m)

Rutenbergia madagassa Geh. & Hampe **End** (alt 1250-1450 m)

Sematophyllaceae

Acroporium megasporum (Duby) M. Fleisch. (alt 1050-2050 m)

Macrohymenium acidodon (Mont.) Dozy & Molk. (alt 1250-2050 m)

Radulina borbonica (Bel.) W.R. Buck (alt 450-1050 m)

Rhaphidorrhynchium rubricaula (Besch.) Broth. (alt 2050 m)

**Sematophyllum crassiusculum* (Brid.) Broth. (alt 250-650 m)

**Sematophyllum schimperi* (Besch.) Broth. (alt 1650 m)

Sematophyllum sinuosulum (Besch.) Broth. (alt 1250-1650 m)

Sematophyllum subpinnatum (Brid.) E. Britton (alt 1850 m)

Trichosteleum debettei var. *laevisetum* Cardot **End** (alt 450-1650 m)

Trichosteleum pervilleanum (Müll.Hal. ex Geh.) W.R. Buck (alt 250 m)

Thuidiaceae

Thuidium assimile (Mitt.) A. Jaeger (alt 650 m)

CONCLUSION

Until our study, 1144 species and infraspecific taxa had been reported from Marline et al. (2012). The new records from this study have increased the total number of bryophyte species of Madagascar to 1188 species and infraspecific taxa. The mosses are the most diverse, comprising 59 families, 187 genera and 760 species and infraspecific taxa. Liverworts comprise 30 families, 86 genera and 425 species and infraspecific taxa. Hornworts are represented by only 2 families, 3 genera and 3 species.

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Appendix 3: Table A

Table A 1: Distribution of number of species per phylogeographic pattern per bryophyte family

Family		END	EMR	AFR	PAL	PAN	MR-Am	MR-As	COS	NA
Adelanthaceae	L						2			
Amblystegiaceae	M	2								
Andreaeaceae	M		1			1				
Aneuraceae	L		1	3	1		2			
Anomodontaceae	M					1				
Archidiaceae	M			1					1	
Arnelliaceae	L				1					
Aytoniaceae	L	1		1		1				
Balantiopsidaceae	L						1			
Bartramiaceae	M	5		9			2		1	
Brachytheciaceae	M	4	4	4		2	1			
Bruchiaceae	M	5	1			1				
Bryaceae	M	8	3	12	4	8	2	1	6	
Calymperaceae	M	2	6	16	1	12	2		1	
Calypogeiaceae	L		1	6	1					
Catagoniaceae	M			1						
Cephaloziaceae	L					1	2			
Cephaloziellaceae	L	2	1	1	1	1				
Cryphaeaceae	M			1	1	1				
Cyathodiaceae	L			1						
Daltoniaceae	M	2	2	4		2				
Dicranaceae	M	39	19	21		3			1	
Ditrichaceae	M	2	1	2		2			1	
Dumortieraceae	L					1				
Entodontaceae	M	7		1						
Erpodiaceae	M	1					1			
Eustichiaceae	M					1				
Fabroniaceae	M	7		2						
Fissidentaceae	M	6	2	21	3	5	2			1
Fossombroniaceae	L									1
Frullaniaceae	L	4	3	20	4	8				1
Frullaniaceae	L									

Funariaceae	M	8	1	1		1			1	
Gigaspermaceae	M			2						
Grimmiaceae	M							3		1
Hedwigiaceae	M			1		1		1		
Hypnaceae	M	14	8	12	1	3	1			
Hypopterygiaceae	M				1	1				
Jamesoniellaceae	L			1	2		2			1
Jungermaniaceae	L			1	2					3
Lejeuneaceae	L	60	25	55	20	32	8	1	2	3
Lembophyllaceae	M	3		2			2			1
Lepidoziaceae	L	5	3	7		2	2			
Leptodontaceae	M		1							
Leskeaceae	M	1								
Leucobryaceae	M	10	3	25	1	5				
Leucodontaceae	M		1	3		1				
Leucomiaceae	M					1				
Lophocoleaceae	L	1	1	4	2	1	4			1
Marchantiaceae	L			2						
Mastigophoraceae	L				1					
Meesiaceae	M								1	
Meteoriaceae	M	4	1	7		2				
Metzgeriaceae	L		1		1	1		1	2	
Mniaceae	M	6		4	1					
Neckeraceae	M	1	1	9	2	2				
Orthotricaceae	M	39	13	10	3	1				
Pallaviciniaceae	L			1			2		1	
Phyllogoniaceae	M					1				
Pilotrichaceae	M	5	3	15		1				1
Plagiochilaceae	L	2	6	10		2	1			
Pleuroziaceae	L				1					
Polytrichaceae	M	2	2	5	1				1	
Porellaceae	L			4	1					
Pottiaceae	M	18	2	10	1	5	5		1	
Prionodontaceae	M			1						
Pterobryaceae	M	10	3	4						
Pterygynandraceae	M	1			1					

Ptychomitriaceae	M			1	1					
Pylaisiadelphaceae	M	16	6	2	1					
Racopilaceae	M	4	1	5				1		
Radulaceae	L	1		5		4			1	
Regmatodontaceae	M				1					
Rhabdoweisiaceae	M					1				
Rhachithecaceae	M					1				
Rhacocarpaceae	M					1				
Rhizogoniaceae	M					1				
Ricciaceae	L			2	1			2		
Rigodiaceae	M					1				
Rutenbergiaceae	M	4	1							
Scapaniaceae	L		1			1		1	1	
Schistochilaceae	L	1					2			
Sematophyllaceae	M	22	6	7	3	1	1			
Serpotortellaceae	M		2							
Sphagnaceae	M	2	3	9	1		1			
Splachnaceae	M			3	1		1			
Stereophyllaceae	M			1			2			
Symphyodontaceae	M					1				
Targioniaceae	L				1			1		
Thuidiaceae	M		1	8	1		1			
Total species		366	141	366	69	120	56	5	29	16

* L: Liverwort; H: Hornwort; M: Mosses; Highlights: most species rich

Table A 2: List of species inventoried in the Marojejy National Park

Latin name	Family	type	250	450	650	850	1050	1250	1450	1650	1850	2050	Distribution
<i>Acanthocoleus madagascariensis</i> (Steph.) Kruijt	Lejeuneaceae	L					1						PAN
<i>Acroporium megasporum</i> (Duby) M. Fleisch.	Sematophyllaceae	M					1	1	1	1	1	1	Af-Am
<i>Acrolejeunea pycnoclada</i> (Taylor) Schiffn.	Lejeuneaceae	L						1					PAL
<i>Adelanthus decipiens</i> (Hook.) Mitt.	Adelanthaceae	L					1	1	1	1			Am-Af
<i>Adelanthus lindenbergianus</i> (Lehm.) Mitt.	Adelanthaceae	L							1	1			Am-Af
<i>Aerobryopsis capensis</i> (Müll.Hal.) M. Fleisch.	Meteoriaceae	M		1				1					AFR
<i>Amazoopsis diplopoda</i> (Pócs) J.J. Engel & G.L.S. Merr.	Lepidoziaceae	L			1								EMR
<i>Anastrophyllum auritum</i> (Lehm.) Steph.	Scapaniaceae	L						1	1		1		AFR
<i>Anastrophyllum piligerum</i> (Nees) Steph.	Scapaniaceae	L						1	1	1	1	1	PAN
<i>Archilejeunea linguifolia</i> Steph.	Lejeuneaceae	L		1									AFR
<i>Bazzania comorensis</i> Steph.	Lepidoziaceae	L						1	1				MNI
<i>Bazzania curvidens</i> Steph.	Lepidoziaceae	L					1	1					END
<i>Bazzania decrescens</i> (Lehm. & Lindenb.) Trevis.	Lepidoziaceae	L					1				1		AFR
<i>Bazzania decrescens</i> subsp. <i>molleri</i> (Steph.) E.W.Jones	Lepidoziaceae	L					1	1	1	1	1	1	AFR
<i>Bazzania decrescens</i> ssp. <i>pumila</i> (Mitt.) Pócs	Lepidoziaceae	L					1	1	1	1	1	1	AFR
<i>Bazzania decrescens</i> subsp. <i>molleri</i> (Steph.) E.W.Jones	Le[idoziaceae	L					1					1	AFR
<i>Bazzania mascarena</i> (Steph.) Herzog	Lepidoziaceae	L								1			MNI
<i>Bazzania nitida</i> (F.Weber) Grolle	Lepidoziaceae	L	1	1		1	1	1	1	1			PAN
<i>Bazzania orbanii</i> Pócs	Lepidoziaceae	L						1	1	1			END
<i>Bazzania praerupta</i> (Reinw., Blume & Nees) Trevis.	Lepidoziaceae	L						1		1	1	1	AFR
<i>Bazzania roccatii</i> Gola	Lepidoziaceae	L				1	1	1					AFR
<i>Calypogeia fissa</i> (L.) Raddi.	Calypogeiaceae	L					1						AFR
<i>Calymperes hispidum</i> Renauld & Cardot	Calymperaceae	M	1	1	1	1							EMR
<i>Calypothecium planifrons</i> (Renauld & Paris) Argent	Pterobryaceae	M				1							AFR
<i>Calymperes taitense</i> (Sull.) Mitt.	Calymperaceae	M	1	1									PAN

<i>Campylopus arctocarpus</i> ssp. <i>madecassus</i> (Besch.) J.-P. Frahm	Leucobryaceae	M								1		1		AFR
<i>Campylopus arcuatus</i> (Brid.) A. Jaeger	Leucobryaceae	M									1	1		AFR
<i>Campylopus flexuosus</i> var. <i>flexuosus</i> (Hedw.) Brid.	Leucobryaceae	M									1			AFR
<i>Campylopus nivalis</i> var. <i>nivalis</i> (Brid.) Brid.	Leucobryaceae	M						1	1			1		PAN
<i>Campylopus robillardei</i> Besch.	Leucobryaceae	M								1				AFR
<i>Caudalejeunea lewallei</i> Vanden BergheN	Lejeuneaceae	L						1						AFR
<i>Cephalozia connivens</i> ssp. <i>fissa</i> Váná	Cephaloziaceae	L				1	1							PAN
<i>Cephaloziella kiaeri</i> (Austin) S.W. Arnell	Cephaloziellaceae	L						1	1					PAL
<i>Cephaloziella vaginans</i> Steph.	Cephaloziellaceae	L						1	1					AFR
<i>Ceratolejeunea belangeriana</i> (Gottsche) Steph.	Lejeuneaceae	L	1							1				PAL
<i>Ceratolejeunea calabariensis</i> Steph.	Lejeuneaceae	L	1				1							AFR
<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn.	Lejeuneaceae	L					1							PAN
<i>Ceratolejeunea diversicornua</i> Steph.	Lejeuneaceae	L			1									AFR
<i>Ceratolejeunea floribunda</i> Stephani	Lejeuneaceae	L					1							AFR
<i>Ceratolejeunea papuliflora</i> Steph.	Lejeuneaceae	L		1										AFR
<i>Ceratolejeunea stictophylla</i> Herzog ex Vanden Berghen	Lejeuneaceae	L	1	1	1	1	1							AFR
<i>Ceratolejeunea variabilis</i>	Lejeuneaceae	L					1	1						MNI
<i>Cheilolejeunea cordistipula</i> (Steph.) Grolle ex E.W. Jones	Lejeuneaceae	L	1		1			1				1		AFR
<i>Cheilolejeunea decursiva</i> (Sande Lac.) R.M. Schust.	Lejeuneaceae	L	1											PAL
<i>Cheilolejeunea intertexta</i> (Lindenb.) Steph.	Lejeuneaceae	L	1	1		1								PAL
<i>Cheilolejeunea krakammae</i> (Lindenb.) R.M. Schust.	Lejeuneaceae	L						1				1		PAL
<i>Cheilolejeunea montagnei</i> (Gottsche) R.M. Schust.	Lejeuneaceae	L					1	1	1	1	1	1	1	AFR
<i>Cheilolejeunea serpentina</i> (Mitt.) Mizut.	Lejeuneaceae	L				1		1						PAL
<i>Cheilolejeunea surrepens</i> (Mitt.) E.W. Jones	Lejeuneaceae	L	1					1						AFR
<i>Cheilolejeunea trifaria</i> (Reinw., Blume & Nees) Mizut.	Lejeuneaceae	L		1			1	1			1	1		PAN
<i>Cheilolejeunea usambarana</i> (Steph.) Grolle	Lejeuneaceae	L				1	1							AFR
<i>Chiloscyphus difformis</i> (Nees) J.J. Engel & R.M. Schust.	Lophocoleaceae	L		1										AFR

<i>Chiloscyphus muricatus</i> (Lehm.) J.J. Engel & R.M. Schust.	Lophocoleaceae	L		1		1	1			1			PAN
<i>Cololejeunea andapania</i> Tixier	Lejeuneaceae	L		1									END
<i>Cololejeunea androphylla</i> var. <i>madecassa</i> Tixier	Lejeuneaceae	L				1							END
<i>Cololejeunea appressa</i> (A. Evans) Benedix	Lejeuneaceae	L	1	1	1	1	1						PAN
<i>Cololejeunea duvignaudii</i> E.W. Jones	Lejeuneaceae	L		1	1								AFR
<i>Cololejeunea elegans</i> Steph.	Lejeuneaceae	L		1									PAL
<i>Cololejeunea floccosa</i> (Lehm. & Lindenb.) Schiffn.	Lejeuneaceae	L			1								PAL
<i>Cololejeunea haskarliana</i> (Lehm. et Lindenb.) Schiffn.	Lejeuneaceae	L	1	1		1							MNI
<i>Cololejeunea lemuriana</i> Tixier	Lejeuneaceae	L	1										AFR
<i>Cololejeunea peponiformis</i> Mizut.	Lejeuneaceae	L				1		1					MNI
<i>Conoscyphus trapezioides</i> (Sande Lac.) Schiffn.	Lophocoleaceae	L						1	1	1	1	1	PAL
<i>Dicranoloma billardieri</i> (Brid. ex Anon.) Paris	Dicranaceae	M						1	1	1	1		PAN
<i>Dicranoloma billardieri</i> var. <i>scopareolum</i> (Müll.Hal.) Thér.	Dicranaceae	M						1	1	1			AFR
<i>Dicranum johnstonii</i> Mitt.	Dicranaceae	M					1	1	1		1		AFR
<i>Diplasiolejeunea cornuta</i> Steph.,	Lejeuneaceae	L							1				AFR
<i>Diplasiolejeunea ensifera</i> Tixier	Lejeuneaceae	L										1	END
<i>Drepanolejeunea cambouena</i> Steph.	Lejeuneaceae	L								1			PAL
<i>Drepanolejeunea cultrella</i> (Mitt.) Steph.	Lejeuneaceae	L								1		1	AFR
<i>Drepanolejeunea madagascariensis</i> (Steph.) Grolle	Lejeuneaceae	L								1			AFR
<i>Drepanolejeunea mascarena</i> (S.W. Arnell) R.L. Zhu et Grolle	Lejeuneaceae	L						1					EMR
<i>Drepanolejeunea physaefolia</i> (Gottsche) Steph.	Lejeuneaceae	L				1	1	1	1	1	1	1	AFR
<i>Drepanolejeunea vandenberghenii</i> Buchbender & Eb. Fisch	Lejeuneaceae	L						1					AFR
<i>Fissidens aristifer</i> Brugg.-Nann.	Fissidentaceae	M				1							EMR
<i>Fissidens asplenioides</i> Hedw.	Fissidentaceae	M	1										PAN
<i>Fissidens punctulatus</i> Sande Lac	Fissidentaceae	M		1		1							PAL
<i>Fissidens serratus</i> var. <i>serratus</i> Müll.Hal.	Fissidentaceae	M	1	1									PAN

<i>Floribundaria floribunda</i> (Dozy & Molk.) M. Fleisch.	Meteoriaceae	M		1	1								AFR
<i>Frullania anderssonii</i> Aongstr.	Frullaniaceae	L	1		1	1							AFR
<i>Frullania angulata</i> Mitt.	Frullaniaceae	L						1					AFR
<i>Frullania apicalis</i> Mitt.	Frullaniaceae	L					1	1	1	1	1		AFR
<i>Frullania apiculata</i> (Reinw. Blume & Nees)	Frullaniaceae	L				1	1	1	1	1	1	1	PAL
<i>Frullania capensis</i> Gottsche	Frullaniaceae	L				1							AFR
<i>Frullania eplicata</i> Stephani	Frullaniaceae	L						1	1			1	AFR
<i>Frullania gabonensis</i> Vanden Berghen	Frullaniaceae	L				1	1						AFR
<i>Frullania grossiclava</i> Steph.	Frullaniaceae	L									1		AFR
<i>Frullania humbertii</i> Vanden Berghen	Frullaniaceae	L						1	1		1		EMR
<i>Frullania letestui</i>	Frullaniaceae	L						1					AFR
<i>Frullania lindenbergii</i> Lehm.	Frullaniaceae	L				1			1		1		AFR
<i>Frullania purpurea</i> Steph.	Frullaniaceae	L	1										AFR
<i>Frullania serrata</i> Gottsche	Frullaniaceae	L						1	1				PAL
<i>Frullania vanden-berghenii</i> Pócs	Frullaniaceae	L						1					NA
<i>Frullania variegata</i> Steph.	Frullaniaceae	L					1						AFR
<i>Gottschea neesii</i> (Mont.) R.M.Schust.	Schistochilaceae	L								1			As-mr
<i>Herbertus dicranus</i> (Taylor ex Gottsche et al.) Trevis.	Herbertaceae	L						1	1	1	1	1	PAN
<i>Herbertus juniperoideus</i> (Sw.) Grolle	Herbertaceae	L						1	1	1	1	1	PAN
<i>Heteroscyphus dubius</i> (Gottsche) Schiffn.	Lophocoleaceae	L	1	1	1	1	1	1					AFR
<i>Heteroscyphus mascarenensis</i> sp. nov.	Lophocoleaceae	L					1					1	MNI
<i>Heteroscyphus spectabilis</i> (Stephani) Schiffn.	Lophocoleaceae	L					1	1	1				AFR
<i>Heteroscyphus splendens</i> (Lehm. & Lindenb.) Grolle	Lophocoleaceae	L						1	1	1	1		PAL
<i>Holomitrium borbonicum</i> Besch.	Dicranaceae	M							1				EMR
<i>Holomitrium gracilisetum</i> Thér.	Dicranaceae	M						1					END
<i>Homaliodendron exiguum</i> (Bosch & Sande Lac.) M. Fleisch.	Neckeraceae	M		1	1								PAL
<i>Hypopterygium tamarisci</i> (Sw. ex Sw.) Brid. ex Müll.Hal.	Hypopterygiaceae	M				1							PAN

<i>Isopterygium intortum</i> (P. Beauv.) A. Jaeger	Pylaisiadelphaceae	M				1							EMR
<i>Isotachis aubertii</i> (Schwaegr.) Mitt.	Balantiopsidaceae	L						1					Am-Af
<i>Iwatsukia jishibae</i> (Steph.) N. Kitag.	Cephaloziaceae	L						1					As-mr
<i>Kurzia capillaris</i> (Sw.) Grolle	Lepidoziaceae	L					1	1	1	1	1	1	Am-Af
<i>Kurzia capillaris</i> ssp. <i>stephanii</i> (Renauld ex Steph.) Pócs	Lepidoziaceae	L								1	1		AFR
<i>Lejeunea anisophylla</i> Mont	Lejeuneaceae	L				1							AFR
<i>Lejeunea caespitosa</i> Lindenb.	Lejeuneaceae	L	1			1							AFR
<i>Lejeunea confusa</i> E.W.Jones	Lejeuneaceae	L	1	1	1	1	1						AFR
<i>Lejeunea eckloniana</i> Lindenb.	Lejeuneaceae	L	1	1		1		1					AFR
<i>Lejeunea flava</i> (Sw.) Nees	Lejeuneaceae	L	1			1		1	1	1			PAN
<i>Lejeunea helenae</i> Pearson	Lejeuneaceae	L				1							AFR
<i>Lejeunea isophylla</i> E.W.Jones	Lejeuneaceae	L		1		1	1		1	1	1		AFR
<i>Lejeunea lomana</i> E.W.Jones	Lejeuneaceae	L							1				AFR
<i>Lejeunea obtusata</i> Gottsche	Lejeuneaceae	L					1	1	1	1			AFR
<i>Lejeunea ramosissima</i> Steph.	Lejeuneaceae	L			1	1	1	1	1	1			AFR
<i>Lejeunea tabularis</i> (Spreng.) Gottsche et al.	Lejeuneaceae	L	1	1		1		1	1				PAN
<i>Lejeunea tuberculosa</i> Steph.	Lejeuneaceae	L		1		1	1	1					PAN
<i>Lejeunea vojtkoi</i> Pócs	Lejeuneaceae	L				1							END
<i>Lepidozia africana</i> Steph.	Lepidoziaceae	L								1			PAN
<i>Lepidozia stuhlmannii</i> Steph.	Lepidoziaceae	L								1			AFR
<i>Lepidozia succida</i> Mitt.	Lepidoziaceae	L				1							AFR
<i>Leptolejeunea maculata</i> (Mitt.) Schiffn.	Lejeuneaceae	L	1										PAN
<i>Leucophanes angustifolium</i> Renauld & Cardot	Calymperaceae	M		1									AFR
<i>Leucoloma bifidum</i> (Brid.) Brid.	Dicranaceae	M		1		1	1	1	1	1			EMR
<i>Leucoloma boivinianum</i> var. <i>boivinianum</i> Besch.	Dicranaceae	M						1					EMR
<i>Leucoloma candidum</i> Broth. In Væltzk.	Dicranaceae	M						1					END
<i>Leucoloma chrysobasilare</i> var. <i>chrysobasilare</i> (Müll.Hal.) A. Jaeger	Dicranaceae	M		1			1						AFR

<i>Leucoloma cinclidotioides</i> Besch.	Dicranaceae	M						1					MNI	
<i>Leucoloma cuneifolium</i> (Hampe ex Müll.Hal. and Geh.) C.H. Wright	Dicranaceae	M								1			AFR	
<i>Leucoloma dichelymoides</i> (Müll.Hal.) A. Jaeger	Dicranaceae	M			1			1	1	1	1		EMR	
<i>Leucoloma fontinaloides</i> Dixon	Dicranaceae	M							1	1			END	
<i>Leucoloma gracilescens</i> Broth.	Dicranaceae	M						1					AFR	
<i>Leucoloma grimmioides</i> P. de la Varde	Dicranaceae	M						1	1	1			AFR	
<i>Leucophanes hildebrandtii</i> Müll.Hal.	Calymperaceae	M	1	1	1	1							AFR	
<i>Leucoloma holstii</i> Broth.	Dicranaceae	M		1		1	1	1					AFR	
<i>Leucobryum isleanum</i> Besch.	Leucobryaceae	M		1	1								AFR	
<i>Leucoloma lepervancheri</i> Besch.	Dicranaceae	M	1	1		1	1	1	1	1			AFR	
<i>Leucoloma madagascariense</i> La Farge	Dicranaceae	M		1			1	1		1			END	
<i>Leucoloma marojeziense</i> La Farge	Dicranaceae	M							1	1			END	
<i>Leucoloma membranaceum</i> La Farge	Dicranaceae	M					1		1				EMR	
<i>Leucoloma ochrobasilare</i> Ren.	Dicranaceae	M		1									EMR	
<i>Leucophanes renaudii</i> Cardot	Calymperaceae	M	1	1	1	1	1			1			AFR	
<i>Leucophanes rodriguezii</i> Müll.Hal.	Calymperaceae	M						1					AFR	
<i>Leucoloma rutenbergii</i> (Geh.) C.H. Wright	Dicranaceae	M				1	1						END	
<i>Leucoloma sanctae-mariae</i> Besch.	Dicranaceae	M							1	1			AFR	
<i>Leucomium strumosum</i> (Hornsch.) Mitt.	Leucomiaceae	M		1	1								PAN	
<i>Leucoloma subchrysobasilare</i> Renauld	Dicranaceae	M					1	1	1	1	1		END	
<i>Leucoloma thraustum</i> Hampe ex Besch.	Dicranaceae	M	1							1	1		END	
<i>Leucoloma thuretii</i> Besch.	Dicranaceae	M										1	END	
<i>Leucolejeunea xanthocarpa</i> (Lehm. et Lindenb.) A.Evans	Lejeuneaceae	L										1	AFR	
<i>Lopholejeunea eulopha</i> (Taylor) Schiffn.	Lejeuneaceae	L				1							PAN	
<i>Lopholejeunea lepidoscypha</i> Kiaer & Pearson	Lejeuneaceae	L										1	END	
<i>Lopholejeunea minima</i> Vanden Berghen	Lejeuneaceae	L				1							MNI	
<i>Lopholejeunea multilacera</i> Steph.	Lejeuneaceae	L	1									1	1	EMR

<i>Lopholejeunea nigricans</i> (Lindenb.) Schiffn.	Lejeuneaceae	L	1	1	1	1	1						PAN
<i>Lopholejeunea onraedtii</i> Vanden Berghen	Lejeuneaceae	L				1	1						END
<i>Lopholejeunea paramultilacera</i> Vanden Berghen	Lejeuneaceae	L	1	1		1							MNI
<i>Lopholejeunea quinquecarinata</i> Vanden Berghen	Lejeuneaceae	L	1	1		1							AFR
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.	Lejeuneaceae	L	1	1	1	1	1						PAN
<i>Lopholejeunea tixieriana</i> Vanden Berghen	Lejeuneaceae	L					1						END
<i>Lopidium struthiopteris</i> (Brid.) M. Fleisch.	Hypopterygiaceae	M		1	1	1							PAL
<i>Macrohymenium acidodon</i> (Mont.) Dozy & Molk.	Sematophyllaceae	M						1	1		1	1	AFR
<i>Macromitrium fasciculare</i> Mitt.	Orthotricaceae	M						1					PAL
<i>Macromitrium fimbriatum</i> (P.Beauv.) Schwaegr,	Orthotricaceae	M							1		1		EMR
<i>Macromitrium mauritianum</i> Schwaegr.	Orthotricaceae	M						1					AFR
<i>Macromitrium serpens</i> (Bruch ex Hook. & Grev.) Brid.	Orthotricaceae	M						1					PAL
<i>Macromitrium sulcatum</i> var. <i>sulcatum</i> (Hook.) Brid.	Orthotricaceae	M						1	1		1		AFR
<i>Mastigolejeunea auriculata</i> (Wilson) Schiffn.	Lejeuneaceae	L				1				1	1		Am-Af
<i>Mastigophora diclados</i> (Brid. ex F.Weber) Nees	Mastigophoraceae	L				1	1	1	1	1	1	1	PAL
<i>Metzgeria crassipilis</i> (Lindb.) A.Evans	Metzgeriaceae	L	1										AFR
<i>Metzgeria furcata</i> (L.) Dumort.	Metzgeriaceae	L		1									SCO
<i>Metzgeria madagassa</i> Steph.	Metzgeriaceae	L	1										PAL
<i>Metzgeria nudifrons</i> Steph.	Metzgeriaceae	L										1	EMR
<i>Microlejeunea africana</i> Steph.	Lejeuneaceae	L	1		1	1	1	1					AFR
<i>Microlejeunea ankasica</i> E.W.Jones	Lejeuneaceae	L					1	1		1			AFR
<i>Microlejeunea inflata</i> Steph.	Lejeuneaceae	L				1							EMR
<i>Microlejeunea oblongistipula</i> (Gottsche) Pearson	Lejeuneaceae	L						1					EMR
<i>Mittenothamnium reptans</i> (Hedw.) Cardot	Hypnaceae	M				1							PAN
<i>Mnioloma fuscum</i> (Lehm.) R.M. Schust.	Calypogeiaceae	L						1			1		PAL
<i>Neckeropsis disticha</i> (Hedw.) Kindb.	Neckeraceae	M		1	1	1							PAN
<i>Neckeropsis madecassa</i> (Besch.) M. Fleisch.	Neckeraceae	M			1								AFR
<i>Orthostichopsis longinervis</i> (Renauld & Cardot) Broth.	Pterobryaceae	M		1		1							EMR

<i>Pilotrichella isleana</i> var. <i>nervosa</i> (Renauld & Cardot) Cardot	Lembophyllaceae	M		1									END
<i>Plagiochila angusta</i> Lindenb.	Plagiochilaceae	L		1									EMR
<i>Plagiochila barteri</i> Mitt.	Plagiochilaceae	L					1	1	1	1			AFR
<i>Plagiochila barteri</i> var. <i>valida</i> (Steph.) Vanden Berghen	Plagiochilaceae	L					1	1	1				AFR
<i>Plagiochila fusifera</i> Taylor	Plagiochilaceae	L				1							NA
<i>Plagiochila granditexta</i> Steph.	Plagiochilaceae	L				1							END
<i>Plagiochila incerta</i> Gottsche	Plagiochilaceae	L		1		1							EMR
<i>Plagiochila kiaeri</i> Gottsche	Plagiochilaceae	L					1						AFR
<i>Plagiochila pectinata</i> Willd. ex Lindenb.	Plagiochilaceae	L				1	1	1	1	1	1		AFR
<i>Plagiochila pinniflora</i> Steph.	Plagiochilaceae	L				1	1						NA
<i>Plagiochila renauldii</i> Steph.	Plagiochilaceae	L					1						MNI
<i>Plagiochila repanda</i> (Schwaegr.) Lindenb.	Plagiochilaceae	L				1	1	1					AFR
<i>Plagiochila terebrans</i> Nees & Mont. ex Lindenb.	Plagiochilaceae	L		1									AFR
<i>Pleurozia gigantea</i> (F.Weber) Lindb.	Pleuroziaceae	L					1	1	1	1			PAL
<i>Plicanthus hirtellus</i> (F. Weber) R.M. Schust.	Scapaniaceae	L						1			1		SCO
<i>Porotrichum elongatum</i> (Welw. & Duby) A. Gepp	Neckeraceae	M		1	1	1							AFR
<i>Porotrichum madagassum</i> Kiaer ex Besch.	Neckeraceae	M		1	1								AFR
<i>Porotrichum usagarum</i> Mitt.	Neckeraceae	M		1		1							AFR
<i>Porotrichum variifolioides</i> (De Sloover) Enroth	Neckeraceae	M		1									AFR
<i>Prionolejeunea grata</i> (Gottsche) Schiffn.	Lejeuneaceae	L	1	1	1	1	1	1	1	1			AFR
<i>Pyrrhobryum spiniforme</i> (Hedw.) Mitt.	Rhizogoniaceae	M		1			1						PAN
<i>Racopilum africanum</i> Mitt.	Racopilaceae	M			1								AFR
<i>Racopilum madagassum</i> Renauld	Racopilaceae	M			1		1						AFR
<i>Radula ankefinensis</i> Gottsche ex Steph.	Radulaceae	L		1									AFR
<i>Radula appressa</i> Mitt.	Radulaceae	L			1	1	1						AFR
<i>Radulina borbonica</i> (Bel.) W.R. Buck	Sematophyllaceae	M	1	1	1		1						PAL
<i>Radula boryana</i> (F.Weber) Mont.	Radulaceae	L		1									Am-Af

<i>Radula fulvifolia</i> (Hook.f. & Taylor) Gottsche et al.	Radulaceae	L		1			1						AFR
<i>Radula madagascariensis</i> Gottsche	Radulaceae	L				1		1			1		AFR
<i>Radula stenocalyx</i> Mont.	Radulaceae	L			1				1	1			Am-Af
<i>Radula voluta</i> Taylor ex Gottsche et al.	Radulaceae	L				1	1						Am-Af
<i>Rhaphidorrhynchium rubricaula</i> (Besch.) Broth.	Sematophyllaceae	M										1	EMR
<i>Riccardia longispica</i> (Steph.) Pearson	Aneuraceae	L								1			AFR
<i>Riccardia nudiflora</i> (Steph.) Grolle	Aneuraceae	L					1	1		1			EMR
<i>Rutenbergia limbata</i> (Hampe) Besch.	Rutenbergiaceae	M				1				1			END
<i>Rutenbergia madagassa</i> Geh. & Hampe	Rutenbergiaceae	M						1	1				END
<i>Schiffneriolejeunea pappeana</i> (Nees) Gradst.	Lejeuneaceae	L						1		1			AFR
<i>Schiffneriolejeunea polycarpa</i> (Nees) Gradst.	Lejeuneaceae	L			1	1							Am-Af
<i>Schlotheimia angulosa</i> P.Beauv.	Orthotricaceae	M						1	1	1	1	1	AFR
<i>Schlotheimia badiella</i> var. <i>helicophylla</i> Besch.	Orthotricaceae	M						1	1	1	1	1	EMR
<i>Schlotheimia badiella</i> Besch.	Orthotricaceae	M						1	1	1			EMR
<i>Schlotheimia excorugata</i> Müll.Hal. ex Cardot	Orthotricaceae	M						1					AFR
<i>Schlotheimia ferruginea</i> (Bruch ex Hook. & Grev.) Brid.	Orthotricaceae	M							1	1	1	1	AFR
<i>Schlotheimia fornicata</i> Duby	Orthotricaceae	M									1		EMR
<i>Schlotheimia microcarpa</i> Geh.	Orthotricaceae	M							1				EMR
<i>Schlotheimia percuspidata</i> Müll.Hal	Orthotricaceae	M								1		1	AFR
<i>Schlotheimia squarrosa</i> Brid.	Orthotricaceae	M									1		EMR
<i>Sematophyllum crassiusculum</i> (Brid.) Broth.	Sematophyllaceae	M	1		1								MNI
<i>Sematophyllum schimperi</i> (Besch.) Broth.	Sematophyllaceae	M								1			AFR
<i>Sematophyllum sinuosulum</i> (Besch.) Broth.	Sematophyllaceae	M						1		1			AFR
<i>Sematophyllum subpinnatum</i> (Brid.) E. Britton	Sematophyllaceae	M									1		PAN
<i>Squamidium brasiliense</i> (Hornsch.) Broth.	Brachytheciaceae	M						1					Af-Am
<i>Syrrophodon albidus</i> ssp. <i>integrifolius</i> (E.B.Bartram) L.T. Ellis	Calymperaceae	M					1						AFR
<i>Syrrophodon gardneri</i> (Hook.) Schwaegr.	Calymperaceae	M						1					PAN

<i>Syrrhopodon gaudichaudii</i> Mont.	Calymperaceae	M						1	1				Af-Am
<i>Syrrhopodon hispidocostatus</i> Renaud & Cardot in Renaud	Calymperaceae	M				1	1	1	1	1			PAN
<i>Syrrhopodon prolifer</i> var. <i>acanthoneuros</i> (Müll.Hal.) Müll. Hal.	Calymperaceae	M				1	1			1			Af-Am
<i>Syrrhopodon prolifer</i> var. <i>prolifer</i> Schwaegr.	Calymperaceae	M						1					PAN
<i>Syzygiella geminifolia</i> (Mitt.) Steph.	Jamesoniellaceae	L						1	1	1			Am-Af
<i>Taxilejeunea conformis</i> (Mont. & Nees) Steph.	Lejeuneaceae	L			1		1						AFR
<i>Telaranea bischleriana</i> Pócs	Lepidoziaceae	L				1		1					EMR
<i>Telaranea coactilis</i> (Spruce) J.J. Engel & G.L.S. Merr.	Lepidoziaceae	L	1	1		1		1					AFR
<i>Telaranea nematodes</i> (Gottsche ex Austin) M. Howe	Lepidoziaceae	L							1				Am-Af
<i>Thuidium assimile</i> (Mitt.) A. Jaeger	Thuidiaceae	M			1								PAL
<i>Thysananthus spathulistipus</i> (Reinw., Blume & Nees) Lindenb.	Lejeuneaceae	L	1			1	1	1					PAL
<i>Trachypodopsis serrulata</i> var. <i>serrulata</i> (P. Beauv.) M. Fleisch.	Meteoriaceae	M		1								1	PAN
<i>Trichosteleum debettei</i> var. <i>laevisetum</i> Cardot	Sematophyllaceae	M	1	1		1	1	1		1			END
<i>Trichosteleum pervilleanum</i> (Müll.Hal. ex Geh.) W.R. Buck	Sematophyllaceae	M	1										AFR

Table A 3: Collected samples, number of species identifications (Id), observed species richness (S_{obs}) number of species occurring at a single elevation and estimated species richness along the then study site transect of the Marojejy National Park

Sites	Samples	Id	S _{Obs}	S _{End}	S _{Sing}	S _{ObsM}	S _{ObsL}	TA	TB	TC	S _{Chao} ± sd	S _{Jack1} ±sd	S _{ace} ± sd
250 m	40	102	43	2	8	12	31	38	32	32	75.63 ± 22.36	51.20 ± 5.09	73.95 ± 21.18
450 m	51	169	62	4	16	30	32	5	56	58	100.91 ± 26.10	78.40 ± 10.18	95.98 ± 22.61
650 m	49	115	37	0	6	18	19	42	41	32	68.00 ± 21.21	43.40 ± 3.82	54.09 ± 11.38
850 m	48	170	74	6	14	21	53	51	60	59	120.33 ± 30.64	89.60 ± 8.91	135.28 ± 41.21
1050 m	45	182	72	8	9	20	52	57	64	61	125.21 ± 35.51	83.10 ± 5.73	123.60 ± 34.37
1250 m	52	260	105	8	24	35	70	82	74	104	161.25 ± 39.07	127.60 ± 15.27	179.03 ± 51.64
1450 m	52	242	72	5	8	29	43	79	79	84	98.40 ± 16.55	82.20 ± 5.09	98.19 ± 16.40
1650 m	52	233	71	8	12	26	44	78	87	68	125.00 ± 33.94	87.80 ± 7.64	110.59 ± 23.75
1850 m	50	183	54	3	8	21	33	66	59	58	81.23 ± 15.01	67.20 ± 5.09	85.08 ± 17.73
2050 m	18	51	27	2	3	7	20	51	0	0	40.50 ± 7.42	32.70 ± 1.91	42.50 ± 8.84

Id = number of identifications, S_{obs} = observed species richness, S_{end} = endemic species, S_{sing}=number of singleton species, S_{obsM} = observed moss species richness, S_{obsL} = observed liverwort species richness TA=0-50 cm, TB=50-100 cm, TC= 100-200 cm, S_{chao} = bias-corrected Chao, S_{jack1} = first order Jackknife, S_{ace} = abundance-based coverage estimator, sd: standard deviation

Table A 4: Liverworts morphological traits

Latin_name	gamlen	gamwid	stdmea	lealen	leawid	pappre	lobpre	tripre	ocepre	oilpre	undpre	sexcon	grofor
<i>Acanthocoleus madagascariensis</i> (Lindenb. & Gottsche) Kruijt	20	1.35	0.12	0.65	0.525	0	1	1	0	0	1	au	mt
<i>Acrolejeunea pycnoclada</i> (Taylor) Schiffn.	25	1.1	0.1025	0.85	0.6	1	1	1	0	1	1	au	mt
<i>Adelanthus decipiens</i> (Hook.) Mitt.	35	2.25	0.225	1	0.4	0	0	1	0	1	0	mo	mt
<i>Adelanthus lindenbergianus</i> (Lehm.) Mitt.	90	2.5	0.275	1.1	0.8	0	0	0	0	1	0	di	mt
<i>Amazoopsis diplopoda</i> (Pócs) J.J. Engel & G.L.S. Merr.	5	1.05	0.155	0.6	0.065	0	0	0	0	0	1	di	mt
<i>Anastrophyllum auritum</i> (Lehm.) Steph.	30	1.1	0.25	0.7	0.5	0	0	0	0	0	0	di	mt
<i>Anastrophyllum piligerum</i> (Nees) Steph.	30	2.25	0.275	1.31	0.875	0	0	1	0	0	0	di	ch
<i>Archilejeunea linguifolia</i> Steph.	15	2.5	0.205	1.405	0.775	0	1	1	0	1	1	au	mt
<i>Bazzania comorensis</i> Steph.	20	1.35	0.215	0.95	0.43	0	0	1	0	1	1	di	ch
<i>Bazzania curvidens</i> Steph.	17.5	1.9	0.24	0.975	0.65	0	0	1	0	1	1	di	ch
<i>Bazzania decrescens</i> (Lehm. & Lindenb.) Trevis.	30	2.8	0.36	1.8	0.85	0	0	1	0	0	1	di	pd
<i>Bazzania decrescens</i> subsp. <i>molleri</i> (Steph.) E.W.Jones	17.5	2	0.175	0.95	0.49	0	0	1	0	1	1	di	pd
<i>Bazzania decrescens</i> ssp. <i>pumila</i> (Mitt.) Pócs	15	1.75	0.195	0.79	0.52	0	0	1	0	1	1	di	pd
<i>Bazzania mascarena</i> (Steph.) Herzog	15	1.25	0.21	0.79	0.52	0	0	1	0	0	1	di	pd
<i>Bazzania nitida</i> (F.Weber) Grolle	15	1.4	0.15	1.1	0.6	0	0	0	0	1	1	di	mt
<i>Bazzania orbani</i> Pócs	15	1.5	0.25	0.725	0.49	0	0	1	0	1	1	di	pd
<i>Bazzania praerupta</i> (Reinw., Blume & Nees) Trevis.	20	2.95	0.33	1.85	1.3	0	0	1	0	1	1	di	pd
<i>Bazzania roccatii</i> Gola	17	2	0.22	1.25	0.8	0	0	1	0	1	1	di	pd
<i>Calypogeia fissa</i> (L.) Raddi.	30	2.5	0.25	1.4	1.15	0	0	0	0	1	1	au	pd
<i>Caudalejeunea lewalli</i> Vanden BergheN	20	1.95	0.155	1.2	0.725	0	0	1	0	0	1	di	mt
<i>Cephalozia connivens</i> ssp. <i>fissa</i> Váná	11.5	1.05	0.155	0.37	0.32	0	0	0	0	0	0	au	mt
<i>Cephalozia kjaeri</i> (Austin) S.W. Arnell	6.5	0.4	0.09	0.15	0.125	0	0	0	0	1	0	au	mt
<i>Cephalozia vaginans</i> Steph.	10	0.2	0.075	0.3	0.075	0	0	0	0	0	1	di	mt
<i>Ceratolejeunea belangeriana</i> (Gottsche) Steph.	32.5	1.25	0.08	0.95	0.71	0	1	1	1	0	1	au	mt
<i>Ceratolejeunea calabariensis</i> Steph.	20	1.25	0.09	0.65	0.425	0	1	0	1	1	1	mo	mt

<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn.	30	1.25	0.09	1.25	0.9	0	1	1	1	1	1	1	au	mt
<i>Ceratolejeunea diversicornua</i> Steph.	30	1	0.1	0.775	0.5	0	1	0	1	1	1	1	au	mt
<i>Ceratolejeunea floribunda</i> Stephani	30	1.6	0.09	0.75	0.475	0	1	0	1	1	1	1	au	mt
<i>Ceratolejeunea papuliflora</i> Steph.	20	1.65	0.1	1	0.65	0	1	0	1	0	1	1	au	mt
<i>Ceratolejeunea stictophylla</i> Herzog ex Vanden Berghen	6	0.9	0.06	0.6	0.4	0	1	0	1	0	1	1	au	mt
<i>Cheilolejeunea cordistipula</i> (Steph.) Grolle ex E.W. Jones	35	1.125	0.075	0.725	0.575	0	1	1	0	1	1	1	au	mt
<i>Cheilolejeunea decursiva</i> (Sande Lac.) R.M. Schust.	12.5	0.575	0.05	0.375	0.26	0	1	1	0	1	1	1	au	mt
<i>Cheilolejeunea intertexta</i> (Lindenb.) Steph.	30	0.85	0.0725	0.46	0.39	0	1	1	0	1	1	1	au	mt
<i>Cheilolejeunea krakammae</i> (Lindenb.) R.M. Schust.	35	0.7	0.08	0.425	0.325	0	1	1	0	1	1	1	di	mt
<i>Cheilolejeunea montagnei</i> (Gottsche) R.M. Schust.	20	1	0.125	0.7	0.525	0	1	1	0	1	1	1	di	mt
<i>Cheilolejeunea serpentina</i> (Mitt.) Mizut.	20	0.9	0.0675	0.425	0.335	0	1	1	0	1	1	1	di	mt
<i>Cheilolejeunea surrepens</i> (Mitt.) E.W. Jones	20	1.1	0.07	0.6	0.4	0	1	1	0	1	1	1	au	mt
<i>Cheilolejeunea trifaria</i> (Reinw., Blume & Nees) Mizut.	20	0.85	0.105	0.575	0.5	0	1	1	0	1	1	1	au	mt
<i>Cheilolejeunea usambarana</i> (Steph.) Grolle	20	0.7	0.095	0.4	0.3	0	1	1	0	1	1	1	au	mt
<i>Chiloscyphus difformis</i> (Nees) J.J. Engel & R.M. Schust.	20	1.75	0.155	1	0.9	0	0	1	0	1	1	1	mo	mt
<i>Chiloscyphus muricatus</i> (Lehm.) J.J. Engel & R.M. Schust.	20	1.75	0.093	0.75	0.375	1	0	0	0	1	1	1	au	mt
<i>Cololejeunea andapania</i> Tixier	3.5	1.5	0.08	0.8	0.5	0	1	0	0	1	0	0	mo	mt
<i>Cololejeunea androphylla</i> var. <i>madecassa</i> Tixier	2	1	0.0525	0.35	0.2	0	1	0	0	1	0	0	au	mt
<i>Cololejeunea appressa</i> (A. Evans) Benedix	1.75	1	0.05	0.4	0.2	1	1	0	1	1	0	0	au	mt
<i>Cololejeunea duvignaudii</i> E.W. Jones	12.5	1.25	0.04	0.6	0.4	1	1	1	0	1	0	0	mo	mt
<i>Cololejeunea elegans</i> Steph.	10	0.75	0.04	0.4	0.22	0	1	1	0	1	0	0	di	mt
<i>Cololejeunea floccosa</i> (Lehm. & Lindenb.) Schiffn.	5	0.5	0.04	0.45	0.28	1	1	1	1	1	0	0	au	mt
<i>Cololejeunea haskarliana</i> (Lehm. et Lindenb.) Schiffn.	5	0.625	0.04	0.4	0.25	1	1	1	0	1	0	0	di	mt
<i>Cololejeunea lemuriana</i> Tixier	5	1.6875	0.08	0.85	0.5	0	1	1	1	1	0	0	mo	mt
<i>Cololejeunea peponiformis</i> Mizut.	1.5	0.6	0.045	0.3	0.2	0	1	0	0	1	0	0	di	pd
<i>Conoscyphus trapezioides</i> (Sande Lac.) Schiffn.	5.5	2.25	0.135	1.2	0.9	0	0	1	0	1	1	1	mo	mt
<i>Diplasiolejeunea cornuta</i> Steph.	15	0.85	0.06	0.7	0.5	0	1	1	1	1	1	1	au	mt

<i>Diplasiolejeunea ensifera</i> Tixier	22.5	1.35	0.11	0.95	0.7	0	1	1	0	1	1	mo	mt
<i>Drepanolejeunea cambouena</i> Steph.	5.5	0.365	0.04	0.21	0.75	0	1	1	1	1	1	mo	mt
<i>Drepanolejeunea cultrella</i> (Mitt.) Steph.	5.5	0.375	0.0375	0.275	0.14	0	1	0	1	1	1	au	mt
<i>Drepanolejeunea madagascariensis</i> (Steph.) Grolle	10	1.25	0.065	0.8	0.4	0	1	1	1	1	1	au	pd
<i>Drepanolejeunea mascarena</i> (S.W. Arnell) R.L. Zhu et Grolle	12.5	1	0.045	0.4	0.275	0	1	1	1	1	1	di	tf
<i>Drepanolejeunea physaefolia</i> (Gottsche) Steph.	5.5	0.5	0.045	0.4	0.215	1	1	1	1	1	1	di	mt
<i>Drepanolejeunea vandenberghenii</i> Buchbender & Eb. Fisch	14	0.525	0.0685	0.41	0.395	1	1	1	1	1	1	di	mt
<i>Frullania anderssonii</i> Aongstr.	55	2.05	0.21	1.46	1.125	0	1	1	0	1	1	di	mt
<i>Frullania angulata</i> Mitt.	125	1.525	0.155	1.4	1.035	0	1	1	0	1	1	di	mt
<i>Frullania apicalis</i> Mitt.	37.5	0.975	0.135	0.75	0.575	0	1	1	0	1	1	di	mt
<i>Frullania apiculata</i> (Reinw. Blume & Nees)	50	1.05	0.155	0.675	0.56	0	1	1	0	1	1	mo	mt
<i>Frullania capensis</i> Gottsche	20	1.025	0.115	0.6	0.425	0	1	1	0	1	1	mo	mt
<i>Frullania epicata</i> Stephani	27.5	1.65	0.205	1.125	0.85	0	1	1	0	1	1	mo	mt
<i>Frullania gabonensis</i>	20	0.703	0.11	0.45	0.35	0	1	1	0	0	0	di	mt
<i>Frullania grossiclava</i> Steph.	30	1.575	0.2	1.175	0.925	0	1	1	0	1	1	di	mt
<i>Frullania humbertii</i> Vanden Berghen	35	1.25	0.14	0.8625	0.7125	0	1	1	0	1	1	di	mt
<i>Frullania latestui</i>	30	1.525	0.175	1.0125	0.85	0	1	1	0	1	1	di	mt
<i>Frullania lindenberghii</i> Lehm.	25	2	0.19	1.11	0.9	0	1	1	0	1	1	mo	pd
<i>Frullania purpurea</i>	25	0.85	0.127	0.55	0.475	0	1	0	0	0	1	di	mt
<i>Frullania serrata</i> Gottsche	80	1.4	0.235	1.04	0.965	0	1	1	0	1	1	mo	mt
<i>Frullania vandenberghenii</i>	28	1.07	85	0.74	0.575	0	1	1	0	0	1	mo	mt
<i>Frullania variegata</i> Steph.	22.5	1.225	0.14	0.875	0.75	0	1	1	0	1	1	di	mt
<i>Gottschea neesii</i> (Mont.) R.M.Schust.	60	6.5	0.18	3.5	1.5	0	0	1	0	1	0	di	mt
<i>Herbertus dicranus</i> (Taylor ex Gottsche et al.) Trevis.	115	2.5	0.2	3.25	1.2	1	0	1	0	0	1	di	mt
<i>Herbertus juniperoideus</i> (Sw.) Grolle	150	2.75	0.23	2.85	0.9	1	0	1	0	0	1	di	mt
<i>Heteroscyphus dubius</i> (Gottsche) Schiffn.	40	2.85	0.25	1.5	0.6	0	0	1	0	1	1	di	mt
<i>Heteroscyphus mascarenensis</i> sp. nov.	25	0.85	0.21	2	1.6	0	0	1	0	1	1	di	mt

<i>Heteroscyphus spectabilis</i> (Stephani) Schiffn.	65	5	0.235	2.25	0.75	0	0	1	0	1	1	di	pd
<i>Heteroscyphus splendens</i> (Lehm. & Lindenb.) Grolle	50	4.25	0.3	2.85	2.1	0	0	1	0	1	1	di	mt
<i>Isotachis aubertii</i> (Schwägr.) Mitt.	35	2.291	0.3	1.25	1.25	0	1	1	0	0	1	di	mt
<i>Iwatsukia jishibae</i> (Steph.) N. Kitag.	12.5	0.275	0.08	0.25	0.125	0	0	0	0	1	1	di	mt
<i>Kurzia capillaris</i> (Sw.) Grolle	40	2	0.085	0.175	0.125	0	0	0	0	0	1	au	ch
<i>Kurzia capillaris</i> ssp. <i>stephanii</i> (Renauld ex Steph.) Pócs	40	2	0.085	0.175	0.125	0	0	0	0	0	1	au	ch
<i>Lejeunea anisophylla</i> Mont.	25	0.85	0.075	0.675	0.45	0	1	1	0	1	1	au	mt
<i>Lejeunea caespitosa</i> Lindenb.	25	0.85	0.075	0.675	0.45	0	1	1	0	1	1	au	mt
<i>Lejeunea confusa</i> E.W.Jones	25	0.6	0.07	0.225	0.165	0	1	0	0	1	1	di	mt
<i>Lejeunea eckloniana</i> Lindenb.	10	0.9	0.085	0.625	0.5	0	1	1	0	1	1	au	mt
<i>Lejeunea flava</i> (Sw.) Nees	25	1.15	0.1	0.625	0.5	0	1	0	0	1	1	au	mt
<i>Lejeunea helenae</i> Pearson	10	0.575	0.06	0.282	0.2	0	1	0	0	1	1	di	mt
<i>Lejeunea isophylla</i> E.W.Jones	40	0.85	0.21	0.6	0.425	0	1	1	0	1	1	di	mt
<i>Lejeunea lomana</i> E.W.Jones	15	0.85	0.09	0.475	0.35	0	1	1	0	1	1	di	mt
<i>Lejeunea obtusata</i> Gottsche	10	0.7	0.0875	0.5	0.4	0	1	1	0	1	1	di	mt
<i>Lejeunea ramosissima</i> Steph.	40	1.15	0.095	0.715	0.47	0	1	1	0	1	1	di	mt
<i>Lejeunea tabularis</i> (Spreng.) Gottsche et al.	25	1.05	0.1	0.575	0.325	0	1	1	0	1	1	au	mt
<i>Lejeunea tuberculosa</i> Steph.	15	0.65	0.05	0.35	0.25	0	1	1	0	1	1	au	mt
<i>Lejeunea vojtkoi</i> Pócs	11	0.6625	0.0695	0.42	0.4	0	1	1	0	1	1	au	mt
<i>Lepidozia africana</i> Steph.	25	0.475	0.18	0.215	0.2725	0	0	0	0	0	1	au	mt
<i>Lepidozia stuhlmannii</i> Steph.	15	0.6	0.205	0.6	0.45	0	0	0	0	1	1	au	mt
<i>Lepidozia succida</i> Mitt.	25	0.565	0.125	0.325	0.25	0	0	0	0	1	1	di	ch
<i>Leptolejeunea maculata</i> (Mitt.) Schiffn.	25	1	0.06	0.65	0.3	0	1	1	1	1	1	di	mt
<i>Leucolejeunea xanthocarpa</i> (Lehm. et Lindenb.) A.Evans	20	1.4	0.125	0.85	0.7	0	1	1	0	1	1	au	mt
<i>Lopholejeunea eulopha</i> (Taylor) Schiffn.	30	1.2	0.18	1.15	0.9	0	1	1	0	1	1	di	mt
<i>Lopholejeunea lepidoscypha</i> Kiaer & Pearson	15	1.15	0.135	0.7	0.525	0	1	1	0	1	1	mo	mt
<i>Lopholejeunea minima</i> Vanden Berghen	10	0.6	0.0925	0.375	0.29	0	1	1	0	1	1	mo	mt
<i>Lopholejeunea multilacera</i> Steph.	20	1.1	0.18	0.845	0.645	0	1	1	0	1	1	mo	mt

<i>Lopholejeunea nigricans</i> (Lindenb.) Schiffn.	20	1.25	0.13	0.675	0.5	0	1	1	0	1	1	au	mt
<i>Lopholejeunea onraedtii</i> Vanden Berghen	10	1.1	0.105	0.615	0.44	0	1	1	0	1	1	mo	mt
<i>Lopholejeunea paramultilacera</i> Vanden Berghen	30	1.66	0.1575	1.0125	0.715	0	1	1	0	1	1	mo	mt
<i>Lopholejeunea quinquecarinata</i> Vanden Berghen	15	0.975	0.1125	0.615	0.4625	0	1	1	0	1	1	mo	mt
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.	15	1.275	0.115	0.74	0.575	0	1	1	0	1	1	mo	mt
<i>Lopholejeunea tixieriana</i> Vanden Berghen	20	1.95	0.155	1.225	0.8	0	1	1	0	1	1	mo	mt
<i>Mastigolejeunea auriculata</i> (Wilson) Schiffn.	50	1.55	0.17	1.1	0.7	0	1	1	0	1	1	au	mt
<i>Mastigophora diclados</i> (Brid. ex F.Weber) Nees	110	0.805	0.26	0.8	0.85	0	0	1	0	0	1	di	tf
<i>Microlejeunea africana</i> Steph.	1.5	0.23	0.0375	0.205	0.155	0	1	0	1	1	1	di	mt
<i>Microlejeunea ankasica</i> E.W.Jones	1.5	0.23	0.0325	0.12	0.1	0	1	0	0	1	1	au	mt
<i>Microlejeunea inflata</i> Steph.	3	0.6	0.05	0.405	0.275	0	1	0	0	0	1	mo	mt
<i>Microlejeunea oblongistipula</i> (Gottsche) Pearson	1.5	0.3	0.03	0.25	0.125	0	1	0	0	1	1	mo	mt
<i>Mnioloma fuscum</i> (Lehm.) R.M. Schust.	7	1.5	0.15	0.75	0.6	0	0	1	0	1	1	di	mt
<i>Plagiochila angusta</i> Lindenb.	45	2.65	0.3	1.15	0.725	0	0	1	0	0	0	di	pd
<i>Plagiochila barteri</i> Mitt.	60	3.8	0.4125	2.2	1.6	0	0	1	0	1	0	di	mt
<i>Plagiochila barteri</i> var. <i>valida</i> (Steph.) Vanden Berghen	60	3.8	0.4125	2.2	1.6	0	0	1	0	1	0	di	mt
<i>Plagiochila fusifera</i> Taylor	20	5.25	0.225	1.55	1.125	0	0	1	0	1	0	di	tf
<i>Plagiochila granditexta</i> Steph.	35	6.6	0.5	3.4	1.55	0	0	1	0	1	0	di	mt
<i>Plagiochila incerta</i> Gottsche	65	3.6	0.34	1.8	1.1	0	0	1	0	0	1	di	mt
<i>Plagiochila kiaeri</i> Gottsche	60	5	0.225	2.75	1.375	0	0	1	0	1	0	di	tf
<i>Plagiochila pectinata</i> Willd. ex Lindenb.	110	5	0.37	2.8	1.4	0	0	1	0	1	0	di	tf
<i>Plagiochila pinniflora</i> Steph.	75	2.75	0.4205	1.25	1.29	0	0	1	0	1	0	di	tf
<i>Plagiochila renauldii</i> Steph.	25	3.1	0.38	1.55	1.3	0	0	1	0	1	0	di	mt
<i>Plagiochila repanda</i> (Schwaegr.) Lindenb.	125	4	0.35	2	1	0	0	1	0	1	0	di	mt
<i>Plagiochila terebrans</i> Nees & Mont. ex Lindenb.	100	4	0.275	2.2	4.18	0	0	1	0	1	0	di	mt
<i>Pleurozia gigantea</i> (F.Weber) Lindb.	75	3.75	0.75	3.5	2.25	0	1	1	0	1	0	au	tf
<i>Plicanthus hirtellus</i> (F. Weber) R.M. Schust.	100	2	0.25	2.5	1	0	0	1	0	1	1	di	ch
<i>Prionolejeunea grata</i> (Gottsche) Schiffn.	25	0.7	0.0675	0.325	0.245	0	1	1	0	1	1	au	mt

<i>Radula ankefinensis</i> Gottsche ex Steph.	20	2	0.17	1.05	0.75	0	1	1	0	1	0	au	mt
<i>Radula appressa</i> Mitt.	35	1.8	0.175	1.15	0.85	0	1	0	0	1	0	di	mt
<i>Radula boryana</i> (F.Weber) Mont.	100	2.65	0.3	1.75	1.6	0	1	1	0	1	0	di	mt
<i>Radula fulvifolia</i> (Hook.f. & Taylor) Gottsche et al.	8	1.5	0.165	0.75	0.65	0	1	0	0	1	0	di	mt
<i>Radula madagascariensis</i> Gottsche	11	1.5	0.11	0.75	0.575	0	1	1	0	1	0	di	mt
<i>Radula stenocalyx</i> Mont.	20	1.45	0.07	0.9	0.8	0	1	1	0	1	0	di	mt
<i>Radula voluta</i> Taylor ex Gottsche et al.	20	1.45	0.12	1	0.75	0	1	1	0	1	0	di	mt
<i>Schiffneriolejeunea pappeana</i> (Nees) Gradst.	37.5	1.85	0.16	1.3	0.875	0	1	1	0	1	1	di	mt
<i>Schiffneriolejeunea polycarpa</i> (Nees) Gradst.	35	1.8	0.14	0.975	0.75	0	1	1	0	1	1	au	mt
<i>Syzygiella geminifolia</i> (Mitt.) Steph.	35	2.75	0.25	1.05	0.75	0	0	1	0	1	0	di	ch
<i>Taxilejeunea conformis</i> (Mont. & Nees) Steph.	30	1.15	0.0975	0.8	0.6	0	1	1	0	1	1	au	mt
<i>Telaranea bischleriana</i> Pócs	4.5	0.8	0.05	0.3	0.0205	0	0	0	0	0	1	au	mt
<i>Telaranea coactilis</i> (Spruce) J.J. Engel & G.L.S. Merr.	4	0.65	0.075	0.975	0.039	0	0	0	0	0	1	au	mt
<i>Telaranea nematodes</i> (Gottsche ex Austin) M. Howe	4	0.65	0.065	0.7	0.0185	1	0	0	0	1	1	au	mt
<i>Thysananthus spathulistipus</i> (Reinw., Blume & Nees) Lindenb.	40	2	0.175	1.5	0.7	0	1	1	0	1	1	au	mt