The diversity of ground bryophyte communities along an altitudinal gradient on La Réunion Island

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Contents

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Abstract

Aim: To compare the α, β and phylogenetic diversity of the ground bryophyte communities along a tropical altitudinal gradient in order to determine which processes govern these assemblages.

Location: La Réunion island (55°39'E; 21°00'S), in the western Indian Ocean.

Methods: The ground bryophyte communities were surveyed along the eastern slope of Piton des Neiges (350 - 3050 m). α, β and phylogenetic diversity along the altitudinal gradient was determined and graphically presented.

Results: The α diversity had two distinct peaks at 1150 – 1350 m and at 2750 m, these corresponded to a dominance in liverwort and moss species, respectively. The phylogenetic diversity along the altitudinal gradient was far greater than is predicted from the null models suggesting that ground bryophyte communities are structured according to "environmental filters". The mid-domain effect and mass effect could not be used to describe the changing diversity along the altitudinal gradient, however a correlation analysis revealed temperature and relative humidity influences the changing α diversity.

Main Conclusions: In conclusion both ecological and evolutionary processes structure the ground bryophyte communities

Introduction

One of the oldest and fundamental patterns in ecology is the decline in biological diversity from equatorial regions polewards, thought primarily to be caused by reducing temperatures and, consequently, degree of productivity (Stevens 1989; Rahbek 1995, Willig *et al.* 2003). Conceptually linked to the latitudinal gradient are altitudinal gradients, which also show a transition from warm to cold climatic conditions. For these, however, three different diversity patterns have been documented. Firstly, an increase in diversity with increasing altitude; a very rare, but nonetheless documented pattern (Bruun *et al.* 2006). Secondly, a monotonic decrease in diversity with increasing altitude; this was thought to be the prevalent pattern, exhibited by all taxa, as it mimics the latitudinal gradient, however Rahbek (1995) showed that this perception was the result of the "citation inbreeding" of early studies. Thirdly, a peak in diversity at mid-altitude; this is by far the most prevalent pattern seen for most organisms along altitudinal gradients (Vetaas and Grytnes 2002; Grytnes 2003; McCain 2004; McCain 2005; Bruun *et al.* 2006).

Understanding the mechanisms underlying these diversity patterns present a significant challenge for ecologists and is the subject of much debate (Rahbek 1995; Willig *et al.* 2003; Lomolino 2001). One of the main concerns is that different taxonomic groups are likely to show different responses along the same altitudinal gradient because of differences in their physiological response to environmental conditions (that change with altitude) and/or because of phylogenetic constraints. Of the various explanations proposed for altitudinal diversity patterns, Mass Effect, Mid-Domain Effect and Abiotic-Biotic Effect are the three most prevalent (Lomolino 2001; Grytnes 2003; Willig *et al.* 2003; McCain 2004; McCain 2005). The Mass/Source-Sink/Rescue Effect is the establishment of species in sites where a self-maintaining population cannot exist (Grytnes 2003). The means by which the mass effect can influence altitudinal biodiversity is through feedback among zonal communities; the diversity will increase in transition zones because of the biotic exchange between two bordering communities/habitat types (Lomolino 2001; Grytnes 2003; Willig *et al.* 2003). Since the most noticeable transition along altitudinal gradient is from forest to alpine, diversity should peak at or near the forest-limit resulting in a mid-altitudinal peak in diversity. The Mid-Domain Effect (MDE) predicts that a random placement of species ranges within a bounded domain (an area circumscribed by a physical barrier such as rivers, oceans, valley basins and mountain summits) will result in a peak in diversity in the middle of the domain because of

the overlapping of many variously sized ranges (Willig *et al.* 2003; McCain 2004; McCain 2005). Studies concerning altitudinal diversity patterns show that MDE as a null model, accounted for some proportion of observed altitudinal diversity patterns (McCain 2004; McCain 2005). Finally, the Abiotic-Biotic Effect predicts that abiotic factors such as temperature (decreases linearly with altitude) and relative humidity (erratic pattern with altitude) will limit diversity in higher altitudes, whereas negative biotic interactions (particularly competition, which decreases in intensity with altitude because of increasing costs) will limit diversity at lower altitudes creating a mid-altitudinal peak in diversity (Lomolino 2001; Grytnes 2003; Willig *et al.* 2003).

In order to assess the composition of ecosystems and the associated ecological processes, one needs to identify an acceptable unit of diversity and a means of measuring it. This, however, proves to be one of ecology's major difficulties (Faith 1992). The two most discussed and applied measures of diversity are alpha and beta diversity. Alpha (α) diversity is defined as the taxonomic richness at a single locality (Sepkoski 1988; Bruun *et al.* 2006). Beta (β) diversity (or turnover) is the taxonomic differentiation between sites, communities, habitats or landscapes (Koleff *et al.* 2003; Graham and Fine 2008). As Koleff *et al.* (2003) and Willig *et al.* (2003) point out, there are numerous means of determining β diversity. However in order to understand the processes that generate variation in diversity, one requires criteria to measure diversity that goes beyond taxonomic richness and turnover (Kluge and Kessler 2011).

In recent years, with the rise of DNA sequencing and phylogenetic analysis, there has been a growing tendency to utilize phylogenetic data to provide a historical framework for quantification and inference of evolutionary and ecological patterns and processes respectively (Horner-Devine and Bohannan 2006; Kembel and Hubbell 2006; Emerson and Gillespies 2008; Graham and Fine 2008; Vamosi *et al.* 2009; Cadotte *et al.* 2010; Kluge and Kessler 2011). α-phylogenetic diversity or point phylogenetic diversity is determined by the sum of the phylogenetic branch lengths (which is proportional to the number of characters or base pair substitutions) connecting all taxa via the minimal spanning path (Faith 1992; Faith 2002; Pennington *et al.* 2006; Forest *et al.* 2007). The various forms of determining β diversity can be adapted to measure Phylobetadiversity by substituting measures of taxonomic relatedness and uniqueness with branch lengths (Bryant *et al.* 2008). In the

absence of phylogenetic information, Faith (1992) proposed the use of the taxonomic hierarchy in order to establish these measures of diversity.

Taxa differ from each other in terms of their position in the phylogenetic tree (Emerson and Gillespies 2008; Kluge and Kessler 2011). Within any community, phylogenetic diversity tends to increase with taxonomic richness until reaching an asymptote where the probability of additional taxa adding new characteristics drops to zero (Emerson and Gillespies 2008; Kluge and Kessler 2011). Various studies have shown two deviations from this random expectation (Kluge and Kessler 2011).

1) Co-occurring taxa are more closely related to each other than is expected from a random sampling of taxa from the larger region pool (Emerson and Gillespies 2008; Kluge and Kessler 2011). This is known as phylogenetic clustering and is the result of 'environmental filters' restricting the taxonomic composition to a limited set of possible characters thus promoting the co-occurrences of closely related taxa (Emerson and Gillespies 2008; Losos 2008; Cavender-Bares *et al.* 2009; Kluge and Kessler 2011).
2) Co-occurring taxa are more distantly related to each other than is expected from a random sampling of taxa from the larger region pool (Emerson and Gillespies 2008; Kluge and Kessler 2011). This is known as phylogenetic overdispersion and is the result of competitive interactions amongst closely related taxa for similar resources promoting the co-occurrences of more distantly related taxa (Emerson and Gillespies 2008; Losos 2008; Cavender-Bares *et al.* 2009; Kluge and Kessler 2011).

Bryophytes are a diverse group of terrestrial plants consisting of three separate lineages; Antherocerotophyta (Hornworts), Bryophyta (Mosses) and Marchantiophyta (Liverworts) (Bell and Hemsley 2000). Difficulties in their identification mean that bryophytes are poorly studied especially in the tropics where their species richness peaks (Ah-Peng *et al.* 2007). However because of the various traits they possess, enabling them to occupy diverse and sometimes stressful environments, bryophytes are found from the equator to the poles, from sea level to mountain summits, making them ideal candidates for studying geographical gradients (Bell and Hemsley 2000; Proctor 2000; Ah-Peng *et al.* 2007). This study seeks to answer what processes govern the ground bryophyte community assemblages and how is this reflected in the diversity along a tropical altitudinal gradient? The aim of this study is to compare the α, β and phylogenetic diversity of the ground bryophyte communities along an

altitudinal gradient on La Réunion Island and test for vegetation boundaries, geometric constraints and climatic effect as explanators affecting. It is hypothesised that biodiversity should peak at mid-altitudes as was reported for corticolous (living on tree bark). Further, it is hypothesised that there will be a strong phylogenetic signal along the altitudinal gradient alluding to an evolutionary process structuring the ground bryophyte communities. Finally, it is hypothesised that the ground bryophyte communities are structured according to Abiotic-Biotic Effect and not according to the Mid-Domain Effect or the Mass Effect. This study is part of the larger-scale project, "Latitudinal and altitudinal gradients of bryophyte communities in the Western Indian Ocean" (BRYOLAT), co-ordinated by the University of La Réunion. The East-African Islands are included among the global biodiversity hotspots (Myers *et al.* 2000) and this study will help to understand the ecological and evolutionary mechanisms underlying these highly diverse, tropical ecosystems.

Methods

Study Area

La Réunion (55°39'E; 21°00'S), the largest island (2512 km^2) in the Mascarene Archipelago, is situated in the western Indian Ocean. It is of recent volcanic origin (2-3 million years ago), created by the presently dormant Piton des Neiges which is located in the centre of the island and at 3070 m is the highest peak (Ah-Peng and Bardat 2005; Ah-Peng *et al.* 2007).

The climate is predominantly tropical, with mean annual temperature ranging from 24°C along the coast to 12°C around 2000 m (Strasberg *et al.* 2005; Lagabrielle *et al.* 2009). Mean annual precipitation ranges from at least 1 m along the coast to >8 m in the mountains and locally 12 m between 1300 m and 1800 m (Strasberg *et al.* 2005; Lagabrielle *et al.* 2009).

Rivals (1952) and Cadet (1980) identified five unique habitat types, while Strasberg *et al.* (2005) broadened this to 20 habitat types. Despite being one of the global biodiversity hotspots along with Madagascar and neighbouring islands, 73% of native vegetation has been transformed since European occupation (from 1665); 36% agriculture, 12% urbanisation and other land use, 25% invasive species (Myers *et al.* 2000; Strasberg *et al.* 2005; Lagabrielle *et al.* 2009). The bryophyte flora is very diverse with 826 species (499 Mosses, 322 Liverworts and 5 Hornworts) having been recorded with an endemism of 8.4% (Ah-Peng *et al.* 2007; Ah-Peng *et al.* 2010).

Study Sites

Species diversity was collected from a transect along the eastern slope of Piton des Neiges with 15 sites at altitudinal intervals of 200 m ranging from 350 m to 3050m (with 100 m separating the 2950 m and 3050 m sites). The location of each site was determined based on the presence of intact vegetation, moderate slope and accessibility. Appendix 1 describes the position of each study site.

The transect crosses eight different vegetation types: Lowland Rainforest (350-750 m), *Pandanus* Wet Thickets (950 m), Sub-montane Windward Forest (1150-1350 m), *Accacia heterophylla* Forest (1550 m), Montane Windward Rainforest (1750 m), *Philippia* Thickets

(1950-2150 m), Shrubland (2350-2550 m), Subalpine Shrubland (2750-3050 m). A description of the vegetation types for La Réunion is given in Strasberg *et al.* (2005).

Sampling Methodology

Sampling was conducted in March of 2008. At each site, two plots of 10 X 10 m were set out. Within each plot, three quadrats of 2 X 2 m were randomly chosen and within each quadrat three samples of 5 x 10 cm of bryophytes were collected from the following ground microhabitats (if present): humicolous (on humus) rupicolous (on rocks) and terricolous (on soil).

A data logger (RHTemp1000IS - MadgeTech, Vermont, USA) within a protective casing was placed one meter off the ground at each site, and measured the temperature (± 0.5 °C) and relative humidity (± 2 %) every hour from 1st June to 10th September 2011.

Sample Processing

Samples were air-dried in paper bags. C. Ah-Peng, J. Bardat, M. Chuah-Petiot, T.A.J. Hedderson and N. Wilding undertook specimen identification. Bryophyte nomenclature followed that of O'Shea (2006) for Mosses, Wigginton (2009) for Liverworts and Hornworts and a list of recorded bryophyte species on La Réunion by Ah-Peng and Bardat (2005).

Data Analysis

Data analysis excluded specimens (< 2 %), which could not be identified, unless otherwise specified.

α Diversity

α diversity was taken as the total number of species recorded per altitude. The number of species and specimens collected at each altitude was plotted, separating the data according to microhabitat and whether the species/specimens were liverworts or mosses.

The range of each species was taken as the altitudinal distance between the lowest and highest altitude at which each species was recorded, and it was assumed that all species occurred throughout their range. Species which occurred at a single altitude were assumed to have an altitudinal range of 100 m (50 m above and 50 m below). The mean altitude occupied

by each species was taken as the mid-point of each species' range. The altitude range profile was constructed according to Ah-Peng *et al.* (in review).

β Diversity

β diversity was determined using Sørenson's similarity index, which is given as

$$Sor_{ij} = \frac{S_{ij}}{(S_i + S_j)\frac{1}{2}}$$

where S_{ij} is the number of taxa common to both altitudes i and j, and S_i and S_j are the total number of taxa found at altitudes i and j respectively (Koleff *et al.* 2003; Bryant *et al.* 2008). Using presence-absence of species (including unidentifiable specimens), Sørenson's similarity index was calculated in R v.2.13.2 (R Development Core Team 2011) using the function 'betadiver' from the package 'vegan' (Oksanen *et al.* 2011) following Bryant *et al.* (2008). The resulting β diversity measures between successive altitudes were plotted against altitude and compared with the phylobetadiversity measures.

Phylogenetic Diversity

The taxonomic hierarchy was used to construct a rudimentary tree depicting the taxonomic relationship between species that was used as a surrogate for phylogeny. The tree was constructed in R v.2.13.2 (R Development Core Team 2011) with the package 'picante' (Kembel *et al.* 2011) using the function 'as.phylo', with each taxonomic level assigned a branch length of one. Species/specimens which lacked any taxonomic classification above species (i.e. could not be assigned to a genus, family or class) had to be excluded in this section of the analysis. This section of the analysis included unidentifiable specimens, which could be assigned to a genus.

In order to determine the phylogenetic community structure at each altitude, the presence-absence of species at each altitude was compared to 999 random assemblages generated using two null models within the function 'ses.pd'. The first null model, *Taxon Shuffle*, shuffles taxa labels across the tips of the phylogeny and the second, *Independent Swap*, randomises the data matrix using the independent swap algorithm (Gotelli 2000) while maintaining species occurrence frequency and sample species richness. These null distributions were used to calculate the standardized effect size of PD (Faith's 1992 measure of α-phylogenetic diversity)

$$Z_{td} = \frac{(TD_{obs} - TD_{null})}{TD_{sdnull}}$$

where TD_{obs} is the observed trait diversity, TD_{null} mean value of the null distribution of random assemblage trait diversities and TD_{sdnull} is the standard deviation of the null distribution, following the methods of Swenson and Enquist (2009). In order to test whether the median Z_{td} was different from the null expectation of zero, a Wilcoxon's test was performed according to the methods of Swenson and Enquist (2009).

Phylobetadiversity was determined using the PhyloSor (Phylogenetic Sørenson's) index, which is given as

$$PhyloSor_{ij} = \frac{BL_{ij}}{(BL_i + BL_j)\frac{1}{2}}$$

where BL_{ij} is the branch length common to both altitudes *i* and *j*, and BL_i and BL_j are the total branch lengths of altitudes *i* and *j* respectively (Koleff *et al.* 2003; Bryant *et al.* 2008). Using presence-absence of species the PhyloSor index was calculated in R v.2.13.2 (R Development Core Team 2011) with the package 'picante' (Kembel *et al.* 2011) using the function 'phylosor'. The resulting phylobetadiveristy measures between successive altitudes were plotted against altitude and compared with the conventional β diversity measures.

Climatic Data and testing MDE and Mass Effect

The average, maximum and minimum temperature and relative humidity was determined for each altitude and plotted. A generalised linear model was used to correlate these climatic variables against total diversity and the diversity of liverworts and mosses.

The α diversity was compared with null model predictions generated by a Monte Carlo simulation procedure – a randomising procedure using sampling without replacement (Mid-Domain Null Programme; McCain 2004). 50 000 simulations with a fixed number of bins (15) were performed, maintaining the range size of species to actual empirical values, but randomizing the midpoint of each range according to the methods of Ah-Peng *et al.* (in review). The 95% randomization curves were plotted with α diversity along the attitudinal gradient, the boundaries of each vegetation types were also indicated.

Results

α Diversity

A total of 1456 bryophyte specimens were collected from 363 samples, giving a total of 221 species (115 liverworts and 106 mosses), belonging to 94 genera and 45 families (Appendix 2). These figures exclude 27 unidentifiable specimens which were placed into six genera and labelled 'unidentifiable' (Appendix 2). A complete identification could not be performed as the specimens were lacking sexual characters and/or the quantity was too small.

Lejeuneaceae is the most species rich family (31 species in 14 families), followed by Dicranaceae (24 species from six genera), Lepidoziaceae (14 species from five genera) and Sematophyllaceae (9 species from seven genera and 3 species which could not be placed into any known genera) (Table 1). Each of the remaining families contributed less than 5% towards the total bryophyte flora and will not be further discussed.

Table 1: The ten dominant (in terms of the number of species) ground bryophyte families, illustrating the classes (L- Liverwort and M-Moss) as well as the total number of genera, species (percentage in terms of total species) and specimens collected along the altitudinal gradient. The altitudinal range is given as the lowest and highest altitude any member from a particular family has been recorded.

Family Name	Class	Number of Genera	Number of Species	Number of Species	Altitudinal Range
Lejeuneaceae	L	14	31 (14.0)	107	550 – 2750 m
Dicranaceae	M	6	24 (10.9)	275	550 – 3050 m
Lepidoziaceae	L	5	14 (6.3)	183	350 – 2350 m
Sematophyllaceae	M	8	12 (5.4)	31	350 – 1750 m
Jungermanniaceae	L	6	10 (4.5)	20	1750 – 2950 m
Aneuraceae	L	1	8 (3.6)	35	950 – 1750 m
Grimmiaceae	M	2	8 (3.6)	158	2350-3050 m
Radulaceae	L	1	8 (3.6)	14	550 – 2150 m
Bryaceae	M	2	7 (3.2)	17	2750 3050 m
Geocalycaceae	L	4	7 (3.2)	57	350 – 1950 m

The total number of bryophyte species (α diversity), along the altitudinal gradient, peaks at 1350 m and 2750 m (Figure 1). The number of specimens collected also peak at these two altitudes. When separating the bryophytes into liverworts and mosses, one can see that the number of liverwort species peak at 1150 m and the number of specimens peak at 1350 m, while the number of moss species peak at 1350 m and 2750 m and the number of specimens peak at 2750 m (Figure 1).

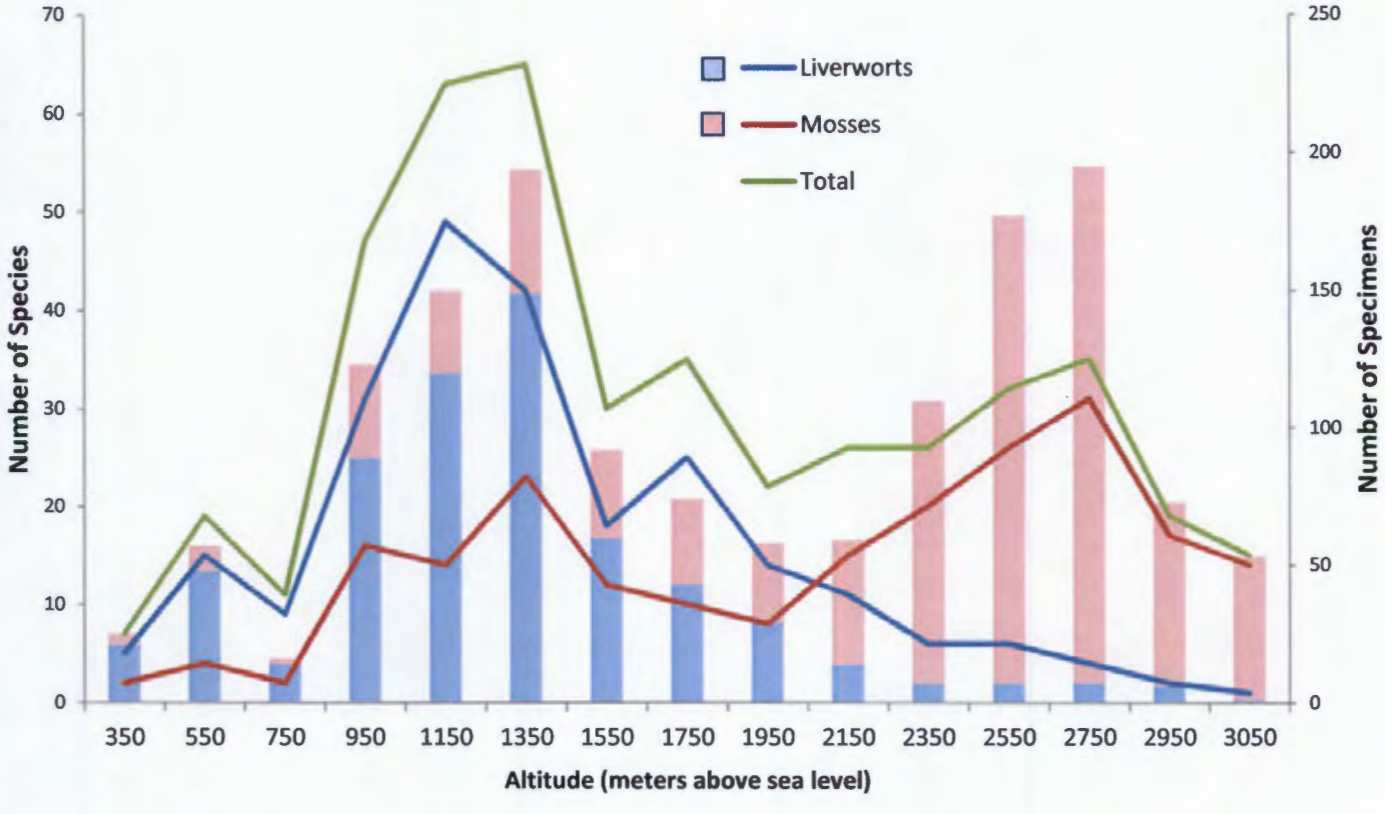

Figure 1: Number of species (Lines) and specimens collected (Bars) of Liverworts (Blue) and Mosses (Red) along the altitudinal gradient. The Solid Green Line indicates the total number of species (α diversity) along the altitudinal gradient.

Humicolous microhabitats occured throughout the altitudinal gradient with the number of samples collected and species richness peaking at 1150 m and 1350 m (Figure 2). Rupicolous microhabitats were rare below 2350 m; the number of samples collected and species richness peaks at 2750 m (Figure 2). Terricolous microhabitats were absent from 750 m and between 1750 m to 2150 m with the number of samples collected and species richness peaking at 1350 m and again at 2550 m and 2750 m (Figure 2).

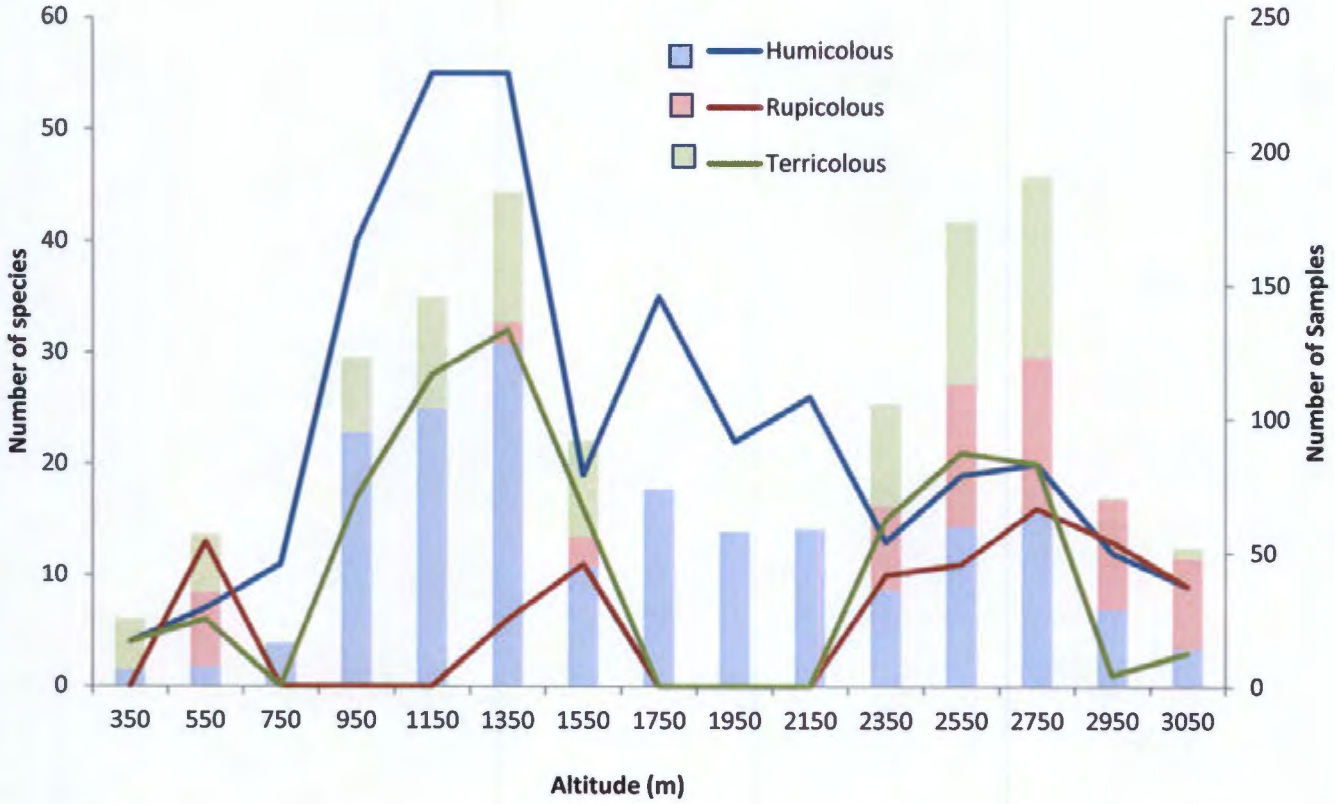

Figure 2: Number of species (Lines) and specimens collected (Bars) within the Humicolous (Blue), Rupicolous (Red) and Terricolous microhabitats along the altitudinal gradient.

The altitudinal range of each species is given in Figure 3. One hundred and twenty-two species (55.2 %) were recorded from a single attitude. These comprise of 65 (56.5 %) liverworts and 57 (53.8 %) mosses. Of these narrow-ranged species, 22 are members of Lejeuneaceae, while Dicranaceae and Sematophyllaceae both have 9 narrow-ranged species. Fifty-four (44.3 %) of these narrow-ranged species occur within the altitudinal range 1000-1300m.

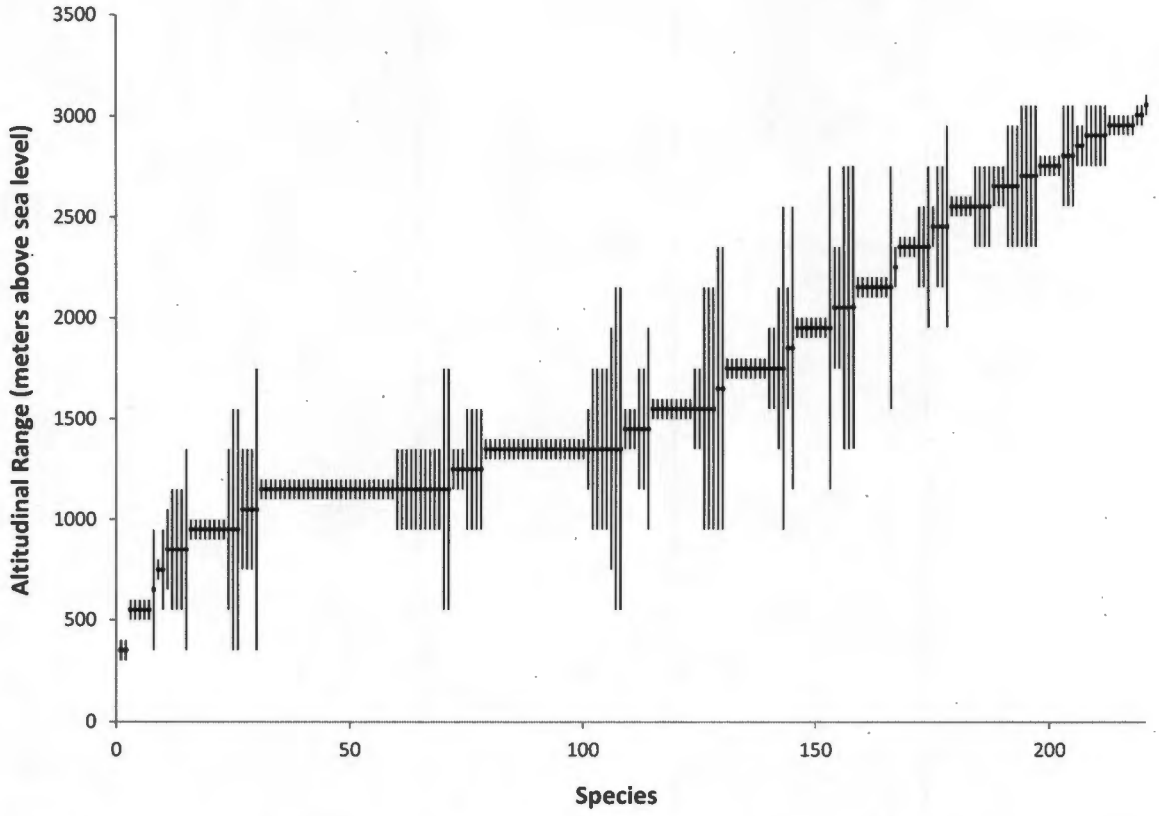

Figure 3: Altitude range profile showing the altitudinal range of all species, arranged according to increasing mid-point, along the altitudinal gradient.

α-phylogenetic diversity

Specimens representing three taxa within the family Sematophyllaceae (Appendix 2) could not be assigned to a genus and therefore were excluded from the phylogenetic diversity analyses.

The median Z_{td} is significantly different from zero when either of the *Taxon Shuffle* null model (Wilcoxon's test; V-stat = 0, $\overline{Z_{td}}$ = -2.67, $p < 0.05$) or the *Independent Swap* null model (Wilcoxon's test; V-stat = 5, $\overline{Z_{td}}$ = -1.92, $p < 0.05$) were used.

According to both null models the phylogenetic diversity is less than expected for the majority of the altitudinal gradient, reaching local minima at 550 m, 1150 m and 2750 m (Figure 4). According to the Independent Swap null model, the phylogenetic diversity is slightly greater than expected at 350 m and 750 m (Figure 4).

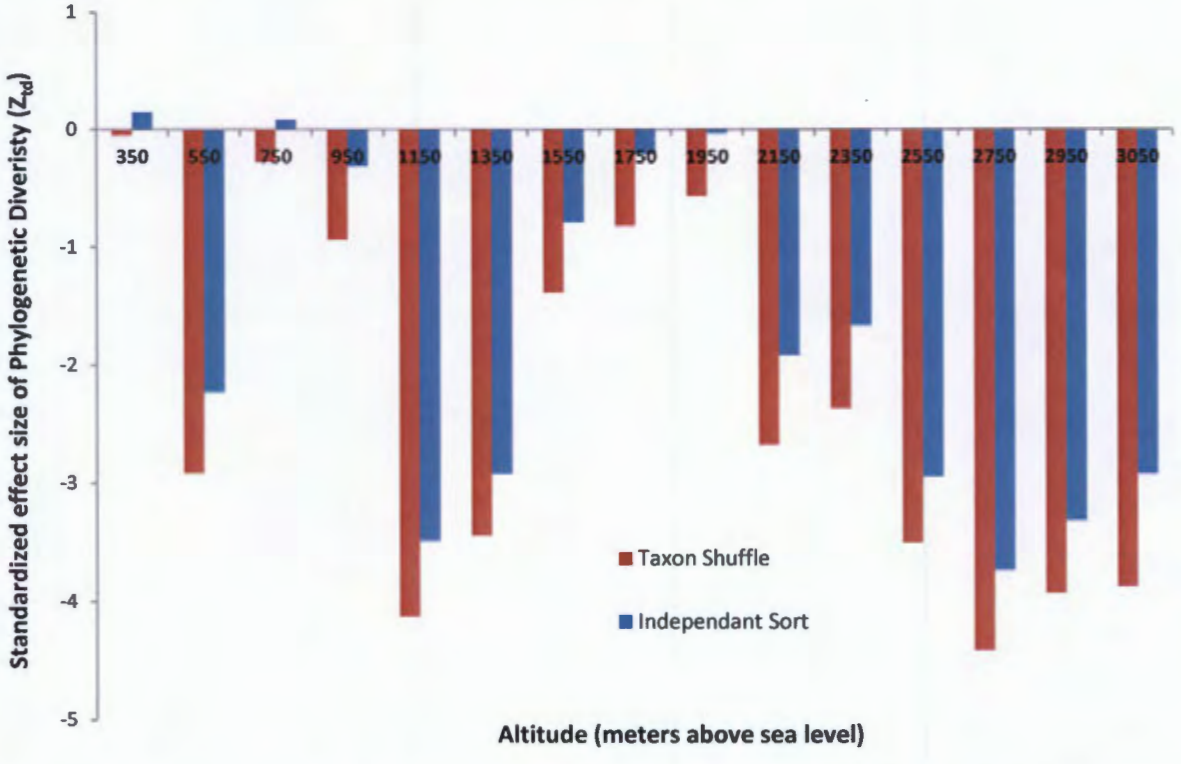

Figure 4: The standardised effect size of phylogenetic diversity (α-phylogenetic diversity) at each altitude as determined using the Taxon Shuffling (Red) and Independent Sorting (Blue) null models.

β Diversity and Phylobetadiversity

The similarity measures determined using the Sørenson's Similarity Index and the PhyloSor Similarity Index yield similar values displaying similar changes along the altitudinal gradient (Figure 5). Similarity tends to increase with altitude. Sudden troughs in similarity occur at 850 m (ranging from 750 m and 950 m), at 2250 m (ranging from 2150 m and 2350 m) and at 2850 m (ranging from 2750 m and 2950 m).

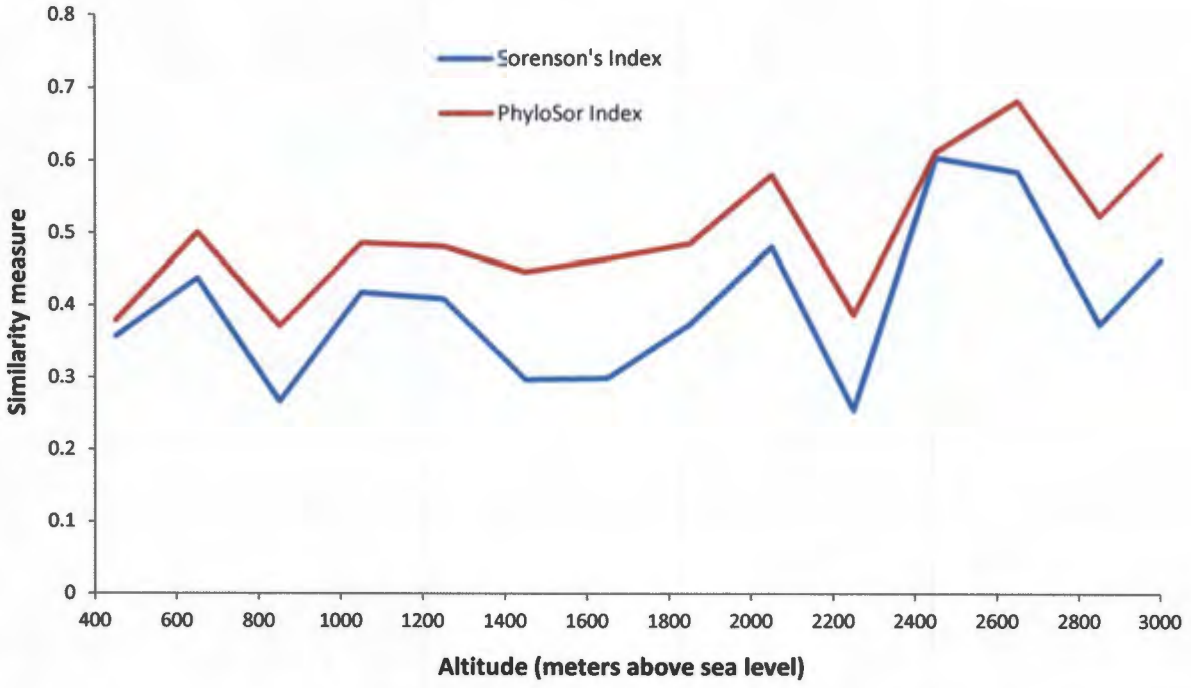

Figure 5: The β diversity along the altitudinal gradient as a similarity measure between neighbouring sites. Blue line indicates measures determined using the Sørenson's Similarity Index and the Red line indicates measure determined using the PhyloSor Similarity Index.

Climatic Data and testing Mid-Domain Effect and Mass Effect

Figure 6 shows the observed number of species along the altitudinal gradient as well as the 95 % prediction curves from 50 000 simulations of the mid-domain null model (McCain 2004). Between 1000 – 1200 m the observed number of species is far greater than predicted and from 2800 m onward the observed number of species is slightly greater than expected, while between 500 – 800 m and 1600 – 2200 m the observed number of species is less than predicted (Figure 6). Within the remaining altitudes, the observed number of species is predicted by the mid-domain null model.

The peaks and troughs within the observed number of species along the altitudinal gradient do not correspond to a boundary between vegetation types, except at 2250 m where there is a slight peak in the number of species between *Philippia* Tickets and Shrubland.

Average temperature declines with altitude; from 18.6°C at 350 m to 6.5°C at 2950 m (Figure 7). The temperature range increases with altitude; from a difference of 10.3°C at 350 m to a difference of 29.7°C at 2950m (Figure 7). The average humidity increases from 90 % at 350 m to approximately 100 % between 550 m to 1750 m and decreases with altitude to 60 % at 2950 m (Figure 7). The maximum recorded humidity is 100 % throughout the altitudinal gradient, while the minimum recorded humidity mimics the curve produced by the average humidity but the values are 30 – 75 % lower (Figure 7).

The results of the generalised linear model, shows that average temperature (R^2=0.51) and relative humidity (R^2=0.35) correlates significantly with the diversity of mosses, while only average relative humidity correlates significantly with liverworts (R^2=0.31).

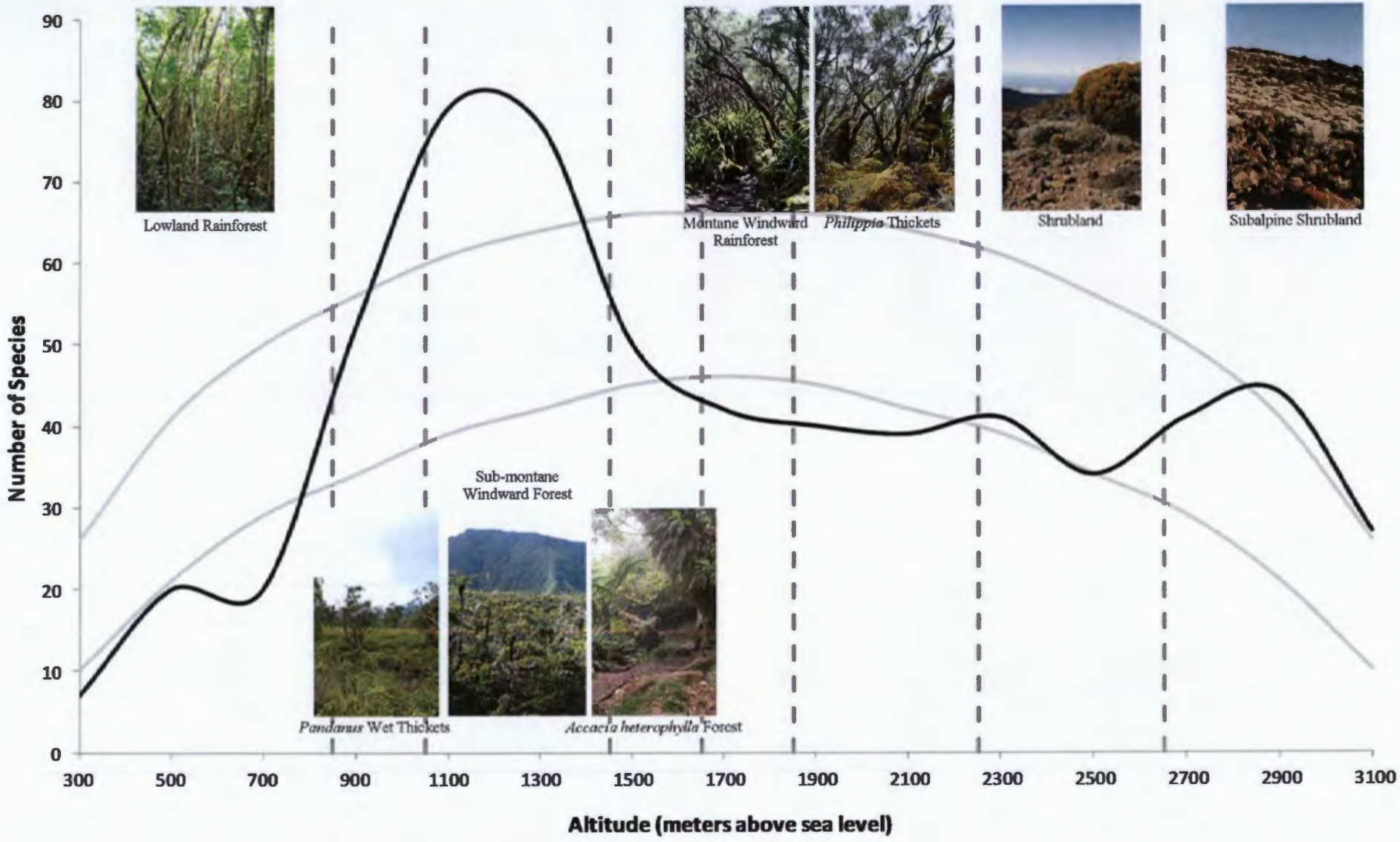

Figure 6: Observed number of species (black line) along the altitudinal gradient and the 95 % prediction curves (grey lines) generated from the mid-domain null model (McCain 2004). The dashed vertical lines indicted the boundary between vegetation types. Inserted pictures give a visual representation of each vegetation type (Strasberg *et al.* 2005).

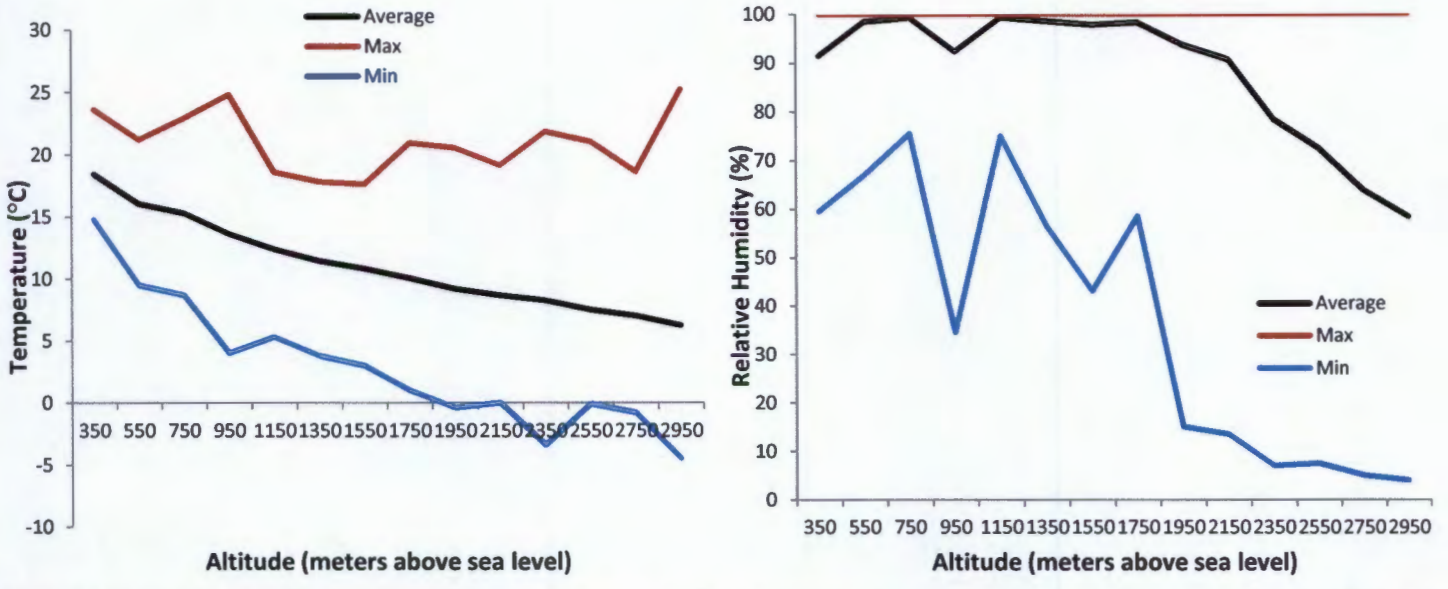

Figure 7: The average (black line), maximum (red line) and minimum (blue line) temperatures (left) and relative humidity (right) recorded along the altitudinal gradient.

Discussion

α diversity

The results show a unimodal relationship between α diversity and altitude for liverworts peaking at 1150 m (Figure 1). Mosses show a bimodal relationship between α diversity and altitude, peaking at 1350 m and 2750 m (Figure 1). Grau *et al.* (2007) found similar results, although the mosses peaked at a lower altitude compared to the liverworts. This contrasts with the results of Wilding (2008), who conducted the same study on La Réunion, focusing on the corticolous microhabitat (bryophytes living on tree bark) and found that α diversity, for both liverworts and mosses, peaked at 1150 m. The lack of a secondary peak in corticolous moss species richness at higher altitude could be attributed to the changing vegetation along the altitudinal gradient, resulting in a reduction in the abundance and stature of host plants.

These patterns in α diversity conform to the initial hypothesis that the biodiversity will peak at mid-altitudes, but at the same time illustrates that different functional groups show different patterns of α diversity; this was also demonstrated in Bruun *et al.* (2006).

There is somewhat of an antagonistic relationship between available humicolous habitats and available terricolous and rupicolous habitats. Forests dominated the lower altitudes (below 2350 m) and the resulting humus, above 950 m, replacing rupicolous and terricolous habitats (Figure 2 and Figure 6; Strasberg *et al.* 2005). When present in these lower altitudes, rupicolous and terricolous habits tend to have a lower α diversity compared to the humicolous habitats (Figure 2).

The lower α diversity between the two peaks at 1150 – 1350 m and 2750 m could be attributed to the lack of terricolous and rupicolous habitats, and therefore a lower number of available niches (Figure 1). However, at 1550 m all three microhabitats are present, yet the diversity is lower than the adjacent peak at 1350 m. Here, low α diversity could be attributed to a change in the vegetation type from the neighbouring Sub-montane Windward Forest (at 1350 m) and the Montane Windward Rainforest (at 1750 m) to *Accacia heterophylla* Forest, which has a more sparse canopy dominated by *A. heterophylla* (Figure 7; Strasberg *et al.* 2005).

The peak in α diversity at 1150 – 1350 m corresponds to the cloud forests, which are said to be favourable living conditions for bryophytes (Porley and Hodgetts 2005; Strasberg *et al.* 2005; Kluge and Kessler 2011). However, the majority of the diversity is described by a high number of narrow-ranged species particularly liverworts from Lejeuneaceae (Figure 3). The second peak in α diversity at 2750 m, within the alpine shrubland, is created through the overlapping of variously sized altitudinal ranges (Figure 3). From a conservation point of view the diversity within the cloud forest require a greater degree of attention because these organisms have nowhere to escape to should this area come under threat (through climate change or habitat destruction).

α phylogenetic diversity

The standardized effect size of phylogenetic diversity is significantly less than zero. These negative values indicated that the species within the ground bryophyte communities tend to be more closely related to one another, than is predicted by null models and can be attributed to the fact the majority of the α diversity arises from a few families (Figure 4 and Table 1). This suggests that these communities are not structured according to neutral processes. Rather, they are under the influence of 'environmental filters', which limits the occupation of ecological niches to organisms exhibiting a particular set of traits (Emerson and Gillespies 2008; Losos 2008; Cavender-Bares *et al.* 2009; Kluge and Kessler 2011). Since related taxa share physiological and ecological tolerances, evolution will favour genetic similarity, reducing the overall genetic diversity. These results conform to the initial hypothesis stating that there will be a phylogenetic signal along the altitudinal gradient which would lead to an evolutionary process structuring the ground bryophyte communities. However, the β diversities contradict the presence of such a process.

β diversities

The β diversities, tends to stay consistently high throughout the altitudinal gradient, suggesting a high degree of similarity in taxonomic composition between successive altitudes (Figure 5). The distinct drop in β diversity at 850 m can be attributed to the change in the vegetation type to that of *Pandanus* Wet Thickets which is known to be quite distinct (in terms of taxonomic composition) from surrounding vegetation types (Figure 5; Strasberg *et al.* 2005). The distinct drop in β diversity at 2250 m can be attributed to the change in the

vegetation type from the montane forests to the alpine shrublands (which also a large change in taxonomic composition) (Figure 5; Strasberg *et al.* 2005).

The similarity measures determined using Sørenson's and PhyloSor produce very similar similarity measures along the altitudinal gradient. Since the only difference between the two measures is that PhyloSor take evolutionary history into account, there is evidence that evolutionary processes (such as speciation and/or extinction events) do not play a significant role in the structuring the ground bryophyte communities (Koleff *et al.* 2003; Bryant *et al.* 2008). However, one must remember that these phylogenetic analyses were based on a rudimentary phylogeny based on the taxonomic hierarchy. Apart from the fact that one needs to be aware that taxonomic levels are assigned branch lengths of one, one must understand how each null model works and what the potential downfalls are. For example in this study *Taxon Shuffle* maintains the relative occurrence of all species across plots, but randomizes the phylogenetic relationships (Kembel *et al.* 2011; Slingsby J pers comm). *Independent Swap* maintains the phylogenetic relationships, species occurrence frequency and sample species richness, but breaks down pattern in the relative occurrence of species (Kembel *et al.* 2011; Slingsby J pers comm). If a more legitimate phylogeny where use, it is highly possible that a different signal would be seen. In the absence of adequate specimens, equipment and time, phylogenies based on taxonomic hierarchy provided an adequate insight into the potential evolutionary processes a play.

Does mass effect structure ground bryophyte communities?

If the mass effect were structuring the ground bryophyte communities then α diversity would peak at the transition between adjacent vegetation types (Lomolino 2001; Grytnes 2003). Since the results show no such pattern, one can conclude that mass effect is not structuring the ground bryophyte community, conforming to the initial hypothesis (Figure 6).

The presence of mass effect is dependent on what vegetation is present and how it changes along an altitudinal gradient. Studies illustrating the presence of mass effect are conducted along altitudinal gradients with very prominent vegetation boundaries (such as between forest and alpine vegetation; Grytnes 2003). This contrasts with the vegetation boundaries on La Réunion, which are far less prominent.

Does mid-domain effect structure ground bryophyte communities?

The mid-domain null model predicted a hump-shaped diversity curve (Figure 6). If the structure of the ground bryophyte communities where reliant on the MDE then one would expect the observed α diversity to fall within the 95 % confidence intervals of this predicated curve (McCain 2004). However, the observed α diversity positively deviates from the null-model at 950 – 1350 m and negatively deviates at 550 – 750 m and 1550 – 2150 m (Figure 6). At these deviations, the level of bryophyte diversity for the ground communites cannot be explained by geometric constraints along this transect. This conforms to the initial hypothesis. However one could argue that the MDE could still be influencing the α diversity away from these deviations.

Wilding's (2008) study focusing on the corticolous microhabitat also had a similar positive deviation from the null model at 1000 – 1300 m and a negative deviation at higher altitudes (> 1900 m) (Wilding 2008). This study too rejected the influence of the MDE on the observed α diversity (Ah-Peng *et al.* in review; Wilding 2008) for corticolous bryophytes along the same bryophytes.

Do abiotic factors structure ground bryophyte communities?

At lower altitudes (< 1750 m), the forest canopy reduces the amount of sunlight reaching the ground and diffusion is retarded by the high humidity, both of which limit photosynthesis (Figure 7; Frahm 1990; Porley and Hodgetts 2005). Additionally, bryophytes are temperature sensitive when hydrated and the increasing temperature moving down the attitudinal gradient poses an increasing strain (Figure 7; Frahm 1990; Porley and Hodgetts 2005).

Alternatively, at higher altitudes (> 1750 m), humidity and temperature decreases with altitude (Figure 7). While desiccation is a common and characteristic feature of bryophytes, it is not universal and many species are desiccation-sensitive and higher altitudes pose an increasing concern (Proctor 2000; Porley and Hodgetts 2005).

The results of the generalised linear model, confirms that mosses and liverworts are significantly correlated to temperature and relative humidity. Abiotic factors can influence the level of diversity at either end of the attitudinal gradient. Theoretically, this should promote a mid-altitudinal peak in the influence conforming to the initial hypothesis that the

abiotic-biotic effect influences the structure of the ground bryophyte communities (minus the biotic component, as it was not analysed in this study) (Lomolino 2001; Grytnes 2003).

Conclusion

The α diversity had two distinct peaks at 1150 – 1350 m and at 2750 m, these corresponded to a dominance in liverwort and moss species, respectively. The phylogenetic diversity along the altitudinal gradient was far greater than is predicted from the null models suggesting that ground bryophyte communities are structured according to "environmental filters". The mid-domain effect and mass effect could not be used to describe the changing diversity along the altitudinal gradient, however a correlation analysis revealed temperature and relative humidity influences the changing α diversity.

In conclusion both ecological and evolutionary processes structure the ground bryophyte communities along the altitudinal transect on La Réunion Island. In the face of climate change and increasing habitat destruction, studies aiming to understand how communities are assembled and the forces that influence their diversity and function will prove essential to managing and resorting Earth's biota (Cavender-Bares 2009).

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Appendix

Appendix 1: Map showing the position and altitude of the study sites (indicated by the yellow markers). At sites where the two plots are separated by more than 200 m, the position of both plots is given separately. Piton des Neiges is indicated by a red marker. Image taken from Google Earth (Google Inc. 2011).

Appendix 2: Table listing the species identified, their occurrences along the altitudinal gradient, their altitudinal range and the midpoint thereof.

Species Name and Author	Altitude (meters above sea level)															Total Occurrences	Altitudinal Range	Midpoint of the Altitudinal Range
	350	550	750	950	1150	1350	1550	1750	1950	2150	2350	2550	2750	2950	3050			
Acroporium megasporum (Duby) M.Fleisch.	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	100	950
Adelanthus decipiens (Hook.) Mitt.	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	100	1350
Aerobryidium subpiligerum var. *majus* (Renauld & Cardot) Wijk & Margad.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Amazoopsis diplopoda (Pocs) J.J.Engel et G.L.S.Merr.	4	7	1	3	7	0	1	0	0	0	0	0	0	0	0	23	1200	950
Anastrophyllum minutum (Schreb.) R.M.Schust.	0	0	0	0	0	0	0	0	0	0	2	1	0	4	0	7	600	2650
Anastrophyllum piligerum (Reinw., Blume & Nees) Steph.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	100	2150
Anastrophyllum sp.1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	100	2350
Andreaea borbonica Besch.	0	0	0	0	0	0	0	0	0	0	0	8	11	0	6	25	500	2650
Andreaea tsaratananae Thér.	0	0	0	0	0	0	0	0	0	0	1	12	12	9	10	44	700	2550
Andrewsianthus aberrans (Nees & Mont.) Grolle	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	100	2150
Andrewsianthus cf. *bilobus* (Mitt.) Grolle	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	100	1950
Aongstroemia julacea (Hook.) Mitt.	0	0	0	0	0	0	0	0	0	0	0	3	4	5	4	16	500	2650
Bartramia gigantea Bory	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	100	2950
Bartramia hampeana ssp. *hampeana* Müll.Hal.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	100	2550
Bartramia longifolia Hook.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	100	2550
Bazzania curvidens Steph.	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	100	1350
Bazzania decrescens ssp. *decrescens*	1	1	1	7	5	17	0	0	0	0	0	0	0	0	0	32	1000	850
Bazzania decrescens ssp. *molleri* (Steph.) E.W.Jones	0	0	0	5	2	1	0	0	0	0	0	0	0	0	0	8	400	1150
Bazzania mascarena (Steph.) Herzog	0	0	0	0	0	0	9	3	3	1	0	0	0	0	0	16	600	1850
Bazzania nitida (F.Weber) Grolle	0	1	0	3	4	7	5	2	1	1	0	0	0	0	0	24	1600	1350
Bazzania praerupta (Reinw., Blume & Nees) Trevis.	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	100	1750

Bazzania roccatii Gola	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2	600	1050
Breutelia borbonica De Sloover	0	0	0	0	0	0	0	0	1	3	0	0	1	0	0	5	800	2350
Breutelia magdalenae De Sloover	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	1200	1550
Breutelia sciuroides Thér. MDG(40)	0	.0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	100	2550
Bryum argenteum var. *argenteum* Hedw.	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	5	300	2750
Bryum dichotomum Hedw.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	100	2750
Bryum sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	100	2850
Calymperes sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Calypogeia afrocaerulea E.W.Jones	0	4	0	3	3	2	14	1	0	0	0	0	0	0	0	27	1200	1150
Calypogeia arguta Nees & Mont.	0	0	0	4	0	1	1	0	0	0	0	0	0	0	0	6	600	1250
Calypogeia fissa (L.) Raddi	0	0	0	4	4	6	0	0	0	0	0	0	0	0	0	14	400	1150
Calypogeia mascarenensis Bischl.	3	3	0	1	0	0	0	0	0	0	0	0	0	0	0	7	600	650
Campylopus arctocarpus ssp. *madecassus* (Besch.) J.-P.Frahm	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	100	1550
Campylopus aureonitens (Müll.Hal.) A. Jaeger	0	0	0	0	0	0	0	0	0	0	12	8	5	1	3	29	700	2550
Campylopus bartramiaceus (Müll.Hal.) Thér.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	100	3050
Campylopus crateris Besch.	0	0	0	0	0	0	0	0	0	1	18	18	10	0	0	47	600	2450
Campylopus flexuosus var. *flexuosus* (Hedw.) Brid.	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	5	1400	2050
Campylopus hildebrandtii (Müll.Hal.) A.Jaeger	0	0	0	0	0	1	0	0	0	0	2	6	5	0	0	14	1400	2051
Campylopus jamesonii (Hook.) A.Jaeger	0	0	0	0	0	1	0	0	2	5	2	1	1	0	0	12	1400	2052
Campylopus nivalis var. *nivalis* (Brid.) Brid.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	100	2150
Campylopus pilifer ssp. *pilifer* Brid.	0	0	0	0	0	0	0	0	0	0	17	5	0	2	0	24	600	2650
Campylopus pyriformis var. *pyriformis* (Schultz) Brid.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	100	1550
Campylopus robillardei Besch.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	100	2350
Campylopus schmidii (Müll.Hal.) A.Jaeger	0	0	0	0	0	0	0	0	0	0	4	6	11	0	0	21	400	2550
Campylopus sp. (Unidentifiable)	0	0	0	0	1	4	0	0	0	0	4	1	4	1	1	16	1900	1950
Campylopus sp.1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	100	2550
Campylopus sp.2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	400	2350
Campylopus thwaitesii (Mitt.) A.Jaeger	0	0	0	0	0	0	5	2	3	1	0	0	1	0	0	12	1200	2150
Cephalozia connivens ssp. *fissa* Váňa	0	0	0	0	0	6	1	0	0	0	0	0	0	0	0	7	200	1450
Cephaloziella kiaeri (Austin) Douin	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	100	1550

Cephaloziella vaginans Steph.	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2	600	2050
Ceratodon purpureus ssp. *convolutus* (Reichardt) Burley	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	6	300	2750
Ceratolejeunea calabariensis Steph.	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	4	600	1050
Ceratolejeunea zenkeri Steph.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Cheilolejeunea montagnei (Gottsche) R.M.Schust.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Cheilolejeunea usambarana (Steph.) Grolle	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Chiloscyphus coadunatus (Sw.) J.J.Engel et R.M.Schust.	1	0	0	0	1	2	2	0	0	0	0	0	0	0	0	6	1200	950
Chiloscyphus lucidus (Spreng. ex Lehm.) J.J.Engel et R.M.Schust.	0	0	0	0	0	2	6	0	0	0	0	0	0	0	0	8	200	1450
Chiloscyphus martianus (Nees) J.J.Engel et R.M.Schust.	0	0	0	1	3	13	3	0	0	0	0	0	0	0	0	20	600	1250
Chiloscyphus muricatus (Lehm.) J.J.Engel et R.M.Schust.	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	3	600	1450
Chiloscyphus regularis Steph	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	100	950
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Cololejeunea xavieri (Lacout. ex Steph.) E.W. Jones	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	100	1150
Cololejeunea zenkeri (Steph.) E.W.Jones	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Colura calyptrifolia (Hook.) Dumort.	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	3	100	1950
Colura sp.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	100	950
Colura tenuicornis (A.Evans) Steph.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	100	1750
Conoscyphus trapezioides (Sande Lac.) Schiffn.	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2	1000	1450
Cryptochila grandiflora (Lindenb. & Gottsche) Grolle	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	400	2350
Cyclodictyon aubertii (P.Beauv.) Kuntze	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Cyclodictyon borbonicum (Besch.) Broth.	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	6	200	1450
Cyclodictyon sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Cylindrocolea gittinsii (E.W.Jones) R.M.Schuster	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Dicranella sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	100	2950
Dicranella subsubulata (Hampe ex	0	0	0	0	0	0	0	0	0	0	1	6	5	0	0	12	400	2550

Müll.Hal.) A.Jaeger																		
Dicranoloma billardierei (Brid.) Paris	0	0	0	1	0	0	0	6	17	14	10	2	0	0	0	50	1600	1750
Diplasiolejeunea cornuta Steph.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Ditrichum difficile (DuBy) M.Fleisch.	0	0	0	0	0	0	0	0	0	0	1	1	1	6	0	9	600	2650
Drepanolejeunea madagascariensis (Steph.) Grolle	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	200	1250
Drepanolejeunea physaefolia (Gottsche) Steph.	0	0	0	1	4	1	0	1	5	2	0	0	0	0	0	14	1200	1550
Ectropothecium regulare (Brid.) A. Jaeger	0	1	1	0	0	0	0	8	0	0	0	0	0	0	0	10	1200	1150
Ectropothecium sp.1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	100	2150
Ectropothecium valentinii Besch.	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	100	950
Entosthodon rottleri (Schwaegr.) Muell. Hal	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	3	200	2450
Entosthodon sp.1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	100	2750
Fissidens intramarginatus (Hampe) Mitt.	0	0	0	1	0	3	6	0	0	0	0	0	0	0	0	10	600	1250
Fissidens porrectus Mitt.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	100	1150
Fissidens sciophyllus fo. *sciophyllus* Mitt.	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	100	1550
Fissidens sp.1	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	5	200	1250
Frullania apicalis Mitt.	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	4	400	1150
Frullania apiculata (Reinw., Blume & Nees) Nees	0	0	1	4	3	2	0	0	0	0	0	0	0	0	0	10	600	1050
Frullania capensis Gottsche	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	3	400	1750
Frullania humbertii Vanden Berghen	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	100	950
Frullania serrata Gottsche	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	100	1750
Gongylanthus ericetorum (Raddi) Nees	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	3	500	2650
Gongylanthus scariosus (Lehm.) Steph.	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	100	2750
Gottschea sphagnoides (Schwägr.) Lindb.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	100	750
Grimmia elongata Kaulf.	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	4	200	2650
Grimmia laevigata (Brid.) Brid.	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	5	200	2650
Grimmia longirostris Hook.	0	0	0	0	0	0	0	0	0	0	1	8	4	2	10	25	700	2550
Grimmia sp.1	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	5	300	2750
Grimmia sp.2	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	5	300	2900
Haplolejeunea sticta Grolle	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Herbertus capensis (Steph.) Sim	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	100	2350
Herbertus dicranus (Taylor ex Gottsche, Lindenb. & Nees) Trevis.	0	0	0	0	0	2	0	3	1	1	0	0	0	0	0	7	800	1750

Herbertus mascarenicus (Steph.) S.W.Arnell ex Váňa	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	100	2150
Heteroscyphus dubius (Gottsche) Schiffn.	0	7	0	0	1	0	0	0	0	0	0	0	0	0	0	8	400	850
Holomitrium borbonicum Besch.	0	0	0	0	0	0	0	1	0	3	1	0	0	0	0	5	600	2050
Hypnum cupressiforme var. *cupressiforme* Hedw.	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	6	100	2750
Isopterygium chryseolum Besch.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	100	1750
Isopterygium intortum (P.Beauv.) A. Jaeger	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	100	1550
Isotachis aubertii (Schwägr.) Mitt.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	100	950
Jaegerina solitaria (Brid.) A.Jaeger	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Jungermannia mildbraedii Steph.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	100	2350
Jungermannia sp.1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	3	200	2850
Kurzia capillaris ssp. *stephanii* (Renauld ex Steph.) Pócs	0	0	0	2	0	0	0	2	0	0	1	0	0	0	0	5	1400	1650
Kurzia capillaris subsp. *capillaris* (Sw.) Grolle	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	100	1750
Lejeunea caespitosa Lindenb.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Lejeunea confusa E.W.Jones	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	3	1400	1850
Lejeunea ecarinata (Steph.) Steph.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Lejeunea eckloniana Lindenb.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Lejeunea flava (Sw.) Nees ssp. flava Schuster	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	5	600	1450
Lejeunea lomana E.W.Jones	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	3	400	1550
Lejeunea rodriguezii (Steph.) Steph.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Lejeunea sp. (Unidentifiable)	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	100	1350
Lejeunea tabularis (Spreng.) Gottsche et al.	0	0	0	0	1	2	1	1	0	0	0	0	1	0	0	6	1600	1950
Lejeunea villaumei (Steph.) Grolle	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Lepidolejeunea delessertii (Nees et Mont.) Grolle	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Lepidopilum hirsutum Besch.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	100	1550
Lepidozia africana Steph.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	100	1950
Lepidozia stuhlmannii Steph.	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	100	1750
Leptodontium flexifolium (Dicks.) Hampe	0	0	0	0	0	0	0	0	0	0	4	6	12	0	0	22	400	2550
Leptodontium pungens (Mitt.) Kindb.	0	0	0	0	0	0	0	0	0	0	0	2	8	0	0	10	200	2650
Leptoscyphus infuscatus (Mitt.) E.W.Jones	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	10	100	1350
Lethocolea congesta (Lehm.) S.W.Arnell	0	0	0	0	0	0	0	0	0	2	0	1	3	0	0	6	600	2450

Leucobryum mayottense Cardot	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Leucobryum sp.1	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	6	100	1350
Leucolejeunea xanthocarpa (Lehm. & Lindenb.) A.Evans	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	5	800	1350
Leucoloma bifidum (Brid.) Brid.	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	3	200	1250
Leucoloma capillifolium Renauld	0	4	1	2	3	0	0	0	0	0	0	0	0	0	0	10	600	850
Leucoloma grandidieri Renauld & Cardot	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	550
Leucoloma lepervancheri Besch.	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	4	100	1150
Leucophanes sp.1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Macromitrium mauritianum Schwägr.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Macromitrium microstomum (Hook. & Grev.) Schwägr.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	100	1950
Mastigophora diclados (Brid. ex F.Weber) Nees	0	0	6	4	4	2	0	5	5	0	0	0	0	0	0	26	1200	1350
Metzgeria furcata (L.) Dumort.	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	100	1150
Metzgeria sp. (Unidentifiable)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Microlejeunea dispar Ast	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	5	100	1150
Microlejeunea inflata Steph.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Microlejeunea kamerunensis Steph.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	100	1150
Mnioloma fuscum (Lehm.) R. M. Schust.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Odontolejeunea lunulata (F.Weber) Schiffn.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	550
Papillidiopsis sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Plagiochila drepanophylla Sande Lac.	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	4	100	1150
Plagiochila flabellata Steph.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	100	1150
Plagiochila integerrima Steph.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	550
Plagiochila pectinata Willd. ex Lindenb.	0	1	0	3	5	4	1	2	3	2	0	0	0	0	0	21	1600	1350
Plagiochila repanda (Schwägr.) Lindenb.	0	3	1	0	1	0	0	0	0	0	0	0	0	0	0	5	600	850
Plagiochila sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Plagiochila terebrans Nees & Mont. ex Lindenb.	0	0	0	1	5	0	3	0	0	0	0	0	0	0	0	9	600	1250
Pleuridium acuminatum Lindb.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	100	2750
Pleuridium sp.1	0	0	0	0	0	0	0	0	0	0	1	6	6	0	0	13	400	2550
Pleurozia gigantea (F. Weber) Lindb.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	100	1950
Plicanthus hirtellus (F.Weber) Mitt.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	100	1950
Pogonatum belangeri (Müll.Hal.) A. Jaeger	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	100	1550

Pogonatum convolutum (Hedw.) P.Beauv.	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	400	1350
Pohlia elongata var. *elongata* Hedw.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	200	2850
Pohlia sp. (Unidentifiable)	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	3	400	2750
Pohlia sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	100	2950
Pohlia sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	100	2950
Pohlia sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	100	2950
Polytrichum commune var. *commune* Hedw.	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	100	1950
Polytrichum piliferum Hedw.	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	3	400	2750
Polytrichum subpilosum P.Beauv.	0	0	0	0	0	0	0	0	1	4	12	20	19	2	0	58	1000	2450
Porotrichum usagarum Mitt.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Prionolejeunea grata (Gottsche) Schiffn.	0	11	0	8	10	6	0	0	0	0	0	0	0	0	0	35	800	950
Ptychanthus striatus (Lehm. Et Lindenb.)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	100	2550
Pyrrhobryum spiniforme (Hedw.) Mitt.	0	0	0	1	5	5	2	1	0	0	0	0	0	0	0	14	800	1350
Pyrrhobryum spiniforme var. *brevifolium* (Besch.) Manuel	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	100	350
Racomitrium membranaceum (Mitt.) Paris	0	0	0	0	0	0	0	0	0	0	8	38	31	25	7	109	800	2550
Racomitrium sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	100	2950
Racomitrium subsecundum (Hook. & Grev.) Mitt. & Wilson	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	4	200	2850
Radula ankefinensis Gottsche ex Steph.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Radula appressa Mitt.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	550
Radula boryana (F. Weber) Mont.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	100	1150
Radula comorensis Steph.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Radula madagascariensis Gottsche	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	3	400	1750
Radula quadrata Gottsche	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Radula stenocalyx Mont.	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	4	600	850
Radula tabularis Steph.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	100	2150
Radulina borbonica (Bél.) W.R.Buck	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	100	350
Rhaphidorrhynchium sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Riccardia amazonica (Spruce) Schiffn. ex Gradst.	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	3	400	1150
Riccardia fastigiata (Lehm.) Trev.	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	100	1550
Riccardia limbata (Steph.) E.W.Jones	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Riccardia longispica (Steph.) Pearson	0	0	0	5	1	9	1	3	0	0	0	0	0	0	0	19	800	1350
Riccardia nudiflora (Steph.) Grolle	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	100	1350

Riccardia obtusa S.W.Arnell	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Riccardia saccatiflora (Steph.) S.W.Arnell	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	4	400	1150
Riccardia sp. (Unidentifiable)	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	4	200	1250
Riccardia sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Schlotheimia badiella Besch.	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	4	200	2250
Sematophyllaceae	0	0	0	2	3	3	0	0	0	0	0	0	0	0	0	8	400	1150
Sematophyllaceae sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Sematophyllaceae sp.2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Sematophyllum schimperi (Besch.) Broth.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	100	1750
Sematophyllum sp.1	0	0	0	2	0	3	0	0	0	0	0	0	0	0	0	5	400	1150
Sphagnum perichaetiale Hampe	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	100	950
Sphagnum sp.1	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0	4	1400	1650
Sphagnum strictum ssp. *pappeanum* (Müll.Hal.) A.Eddy	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	100	2150
Sphagnum tumidulum var. *tumidulum* Besch.	0	0	0	3	0	0	0	6	0	3	0	0	0	0	0	12	1200	1550
Stictolejeunea balfourii (Mitt.) E.W.Jones	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	550
Symphyogyna brasiliensis Nees & Mont.	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	4	400	1150
Syrrhopodon apertifolius Besch.	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	100	950
Syrrhopodon hispidocostatus Renauld & Cardot in Renauld	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	4	400	1150
Syrrhopodon sp.1	0	0	0	3	1	1	0	0	0	0	0	0	0	0	0	5	400	1150
Syzygiella geminifolia (Mitt.) Steph.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	100	1750
Telaranea coactilis (Spruce) Engel & Merr.	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	3	400	1550
Telaranea diacantha (Mont.) Engel et Merr.	12	5	1	10	5	5	0	1	0	0	0	0	0	0	0	39	1400	1050
Telaranea nematodes (Gottsche ex Austin) M.Howe	0	0	0	3	1	12	6	1	0	0	0	0	0	0	0	23	800	1350
Telaranea sp. (Unidentifiable)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	100	1350
Thuidium tamariscinum (Hedw.) Bruch, Schimp. & W.GümBel	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	4	100	1750
Trichosteleum adhaerens (Besch.) Kindb.	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	100	1550
Trichosteleum debettei (Besch.) Kindb.	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	6	400	750
Warburgiella sp.1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	100	1150
Total Number of Species:	227									**Total Occurrences:**						1456		