FUNCTIONAL TRAITS AS DRIVERS OF BRYOPHYTE SPECIES DISTRIBUTION ALONG A TROPICAL ELEVATIONAL GRADIENT

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Mountain rainforest at 1750 m, Piton des Neiges.

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ABSTRACT

Patterns of functional trait diversity of corticolous liverworts on a tropical altitudinal gradient were compared and related to changes in temperature and humidity. The study was conducted along a transect on the Piton des Neiges volcano, situated in the centre of on La Réunion island. Liverwort assemblages were surveyed every 200 m (from 350 to 2750 m a.s.l) in two 10 X 10 m plots. Functional traits were recorded and measured for all the liverwort species occurring on the gradient. Temperature and humidity data loggers were set up at each site to record hourly data from May to September 2011. Regression and Principal Component analyses were conducted. Results showed a decrease in both temperature and humidity with altitude. Ten of the 13 functional traits were found to have significant regressions on altitude. The first four principal components accounted for more than 80% of the covariation and were all found to have significant regressions with altitude. Six cluster groups were formed based on associated functional traits, showing significant differences in altitudinal ranges. Stepwise multiple regression analyses revealed significant relationships between traits and climatic variables. This study provides evidence for the existence of patterns in corticolous liverwort species distribution according to associated functional traits, and particularly in relation to climatic conditions. Advances in functional trait research can contribute towards the prediction of climate change effects on biodiversity along altitudinal and latitudinal gradients.

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INTRODUCTION

Changes in species diversity and richness along altitudinal gradients have been observed and studied since the origin of biogeography (Lomolino, 2001). The environmental factors that change along altitudinal gradients, such as climate, productivity and energy, affect the distribution of many species and communities, and are believed to mirror changes in latitudinal gradients (Lomolino, 2001). For this reason, studies investigating species distributions on altitudinal gradients contribute to the general understanding of species diversity and distribution around the world (Korner, 1999).

Inter- and intraspecific variation among plants has long been recognized as an important part in understanding ecology and evolutionary biology. Variability occurs for many aspects of a species' functioning in a particular environment, such as growth, development, physiology and life history. These variations are often related to environmental constraints, and are expressed in the form of "traits" (Cianciuruso *et al.*, 2009). "Functional traits", are defined as any morphological, physiological or phenological characteristic of an organism that affects its individual performance (Violle *et al.*, 2007). Functional traits influence an organism's fitness by controlling the above-mentioned aspects, thereby controlling the survival, growth and reproduction of an individual.

Indeed, the quantification of interspecific variation in functional traits has allowed a more comprehensive understanding of plant trade-offs and relationships at regional and global scales. This has contributed to important advances in the study of comparative plant ecology in the last few decades (Cornelissen *et al.*, 2007). The concept of "functional traits" is now a useful tool in devising functional classifications of organisms, measuring the functional diversity of a community and assessing species effects on ecosystems (Violle *et al.*, 2007).

Tropical, montane forests are among the most biodiverse regions in the world (Kessler, 2001). Many of these forests occur on isolated, oceanic islands and are therefore removed from the influences (e.g. migration, alien invasion) of surrounding continental vegetation. Due to the small area these forests occupy, they are also very prone to extinction and sensitive to disturbances. These systems are valuable to researchers as they represent open laboratories (pristine, real world systems) which can be used to study the effects of climate change,

particularly regarding changes in plant species composition and distribution along altitudinal gradients.

Bryophytes (mosses, liverworts and hornworts) are the most diverse group of land plants after the angiosperms and found in all corners of the world, representing an enormous range of biomes and habitat gradients. On tropical, oceanic islands such as La Réunion, bryophytes are abundant and diverse (the number of species greater than that of angiosperms). Despite this, very little is known about the functional traits of bryophytes and their contribution to ecosystem processes, as most advances in functional trait research have been based almost exclusively on vascular plants. Very little attention has been given to bryophytes and other non-vascular cryptograms (Cornelissen *et al.*, 2007). The exclusive bias towards the study of vascular plants in the literature is somewhat ironic, as bryophytes play a major role in the functioning of tropical (and other) ecosystems: they contribute greatly to the above ground biomass, affect biogeographical and soil nutrient processes, play a role in feedback mechanisms and compete with vascular plants (Cornelissen *et al.*, 2007).

In today's world, where climate change and accelerating rates of species extinction are of major concern, much emphasis is being placed on understanding the impacts of global change on species distribution and ecosystem functioning (Gernier *et al.*, 2004). Bryophytes are believed to be facing great changes in their abundance, biomass and composition as a result of global change. These changes would result from climate warming-induced influences on hydrology, soil N and/or P availability, vascular plant expansions and more (Cornelessin *et al.*, 2007). Research on functional traits is critical for understanding the response of bryophytes to these changes, as it would seem that these responses depend on the species or functional group.

It is crucial to understand how traits vary among species in relation to their altitudinal range, as this would provide an understanding of the direction and magnitude of change that the various functional groups may experience, and would allow a more solid understanding of their distribution in the long term. Research on interspecific variation in key traits could help to formulate and test predictions about such changes and their feedbacks (Murray *et al.*, 2002; Cornelissen *et al.*, 2007).

One of the most remarkable features of bryophytes is their ability to dry up completely, losing virtually all their intracellular water and shutting down all metabolic activity, only to recover normal growth and function upon rehydration (Proctor *et al.*, 2007). Their small size and small surface-area to volume ratio, as well as their lack of storage tissue and a leaf cuticle, results in bryophytes drying out very quickly. They are also exposed to a much wider range of microclimates within a particular habitat, and with that a range of humidity, temperature and wind speed gradients. Therefore, all bryophytes need to be able to survive desiccation to some degree, as there is no guarantee that they will be kept constantly moist all the time (Proctor *et al.*, 2007).

Bryophytes are poikilohydric organisms, which mean that they are unable to maintain constant water potential through regulation of water loss (Raven, 1995). Therefore, the plants must be able to prevent the fluctuation of water within their cells by associating closely with external capillary water, in order for the cells to remain turgid (Proctor *et al.*, 2007). If this water evaporates, the cells quickly dry out and metabolism ceases. Therefore, a number of morphological traits of bryophytes are adapted to regulate the distribution and movement of this important extracellular water by acting through surface tension (Proctor, 1979, 2002).

A number of papers in the literature describe some morphological traits that control the movement of this extracellular water (Schofield, 1981; Proctor, 2000; Kürschner, 2004). For example, the different growth forms of bryophyte gametophytes represent different strategies related to water availability. Compact cushions or thick mats are most commonly found in well-drained habitats as they are the slowest to dry out (Proctor, 1981) and would enable the plant to stay wetter for longer. Isolated or dendroid forms are more commonly found in habitats where relative humidity is much higher because these forms dry out quickly. Proctor *et al.* (2007) suggest that the bryophyte growth forms probably reflect evolutionary tradeoffs between coping with water loss and maximising light interception.

Leaf surface papillae are also important adaptations in bryophytes which appear to aid water uptake by creating capillary channels on the leaf surface. Attenuate leaf apices seem to serve the same role as hyaline hair points in preventing rapid water loss, by reflecting sunlight and increasing the absorption of condensed water vapour from early morning fog and dew. These and other hydrology-related traits are important for the plants as they affect their desiccation

tolerance, water-retention capacity and nutrient fluxes. These processes are all vitally important to the physiologies of the plants, and affect their responses to disturbances and changes in climate (Cornelissen *et al.*, 2007). A number of bryophyte traits are not well understood in terms of the function they perform. For example, oil bodies in liverworts are membrane-bound organelles that contain high concentrations of chemical compounds. They have been linked to protection from environmental hazards such as UV radiation (Crandall-Stotler & Stotler, 2000), but the mechanisms are still not yet fully understood.

Indeed, there are many papers in the literature that describe numerous morphological traits of bryophytes, and possible functions these traits may carry out, but these papers are largely speculative, and few have actually tested the traits for their associated functions. Many of the studies are largely based on quantitative data and often on only a few species. This makes it difficult to scale-up and detect patterns that can be broadly applied. No study has yet looked at the variation in functional traits of bryophytes along a tropical altitudinal gradient in relation to altitude as well as climatic variables.

This study is part of the large-scale project "Latitudinal and altitudinal gradients of bryophyte communities in the western Indian Ocean - (BRYOLAT)", co-ordinated by the University of La Réunion. This project aims to contribute to an understanding of the ecological and historical mechanisms underlying the high species richness of the western Indian Ocean islands, by studying one of the major plant groups in this geographical area: bryophytes.

The objectives of the present study are to (i) compare patterns of functional trait diversity in corticolous liverwort species along a tropical altitudinal gradient, and relate these patterns to changes in temperature and humidity along the same gradient and (ii) to use these data to assess whether there are particular functional traits that are associated with species occurring in a specific distribution range. It is expected that functional trait diversity will drive the species richness and distribution of liverworts along the altitudinal gradient, according to changes in water availability, represented by the temperature and humidity of the environment.

METHODS

Study area

This study was conducted on La Réunion, the largest island of the Mascarene archipelago in the western Indian Ocean (55°39'E, 21°00'S). It is a volcanic island of relatively recent origin (2-3 million years), and spans an area of approximately 2512 km^2 (figure 1). In the centre of the island lies the dormant volcano, Piton des Neiges, reaching its highest peak at an altitude of 3070 m (Ah-Peng *et al.*, 2007).

La Réunion has been recognized as a global biodiversity hotspot (Myers *et al.*, 2000). Thirty per cent of the native vegetation is well conserved, and large areas of tropical rainforest remain intact (Strasberg, 2005). Therefore, the ecosystem diversity is remarkably high, given the small area of the island. The bryophyte flora is very diverse, with 499 moss taxa, 322 liverwort taxa and 5 hornwort species recorded to date (Ah-Peng *et al.*, 2010). This high diversity may be due to the varying topography and microclimates on the island, as well as the variable precipitation regimes, resulting in a range of diverse habitats (Ah-Peng *et al.*, 2007).

The climate is predominantly tropical, with summer rainfall occurring from November to April, and a cooler, drier winter from June to September. Mean annual rainfall varies according to the position on the island, ranging from 500-1500 mm along the drier, western coast to 1500 - > 8000 mm on the eastern, windward side of the island and at higher altitudes. Mean annual temperatures range from 24°C along the coast to 12°C at around 2000 m (Strasberg *et al.*, 2005).

Study site and fieldwork

Sampling was conducted along an altitudinal transect on the Eastern slope of Piton des Neiges between 350 m and 3070 m a.s.l. Fourteen sites at intervals of 200 m were chosen, their location determined by the presence of intact forest, moderate slope and accessibility. Fieldwork was carried out in March 2008, over a period of 3 weeks. At each site, 2 plots of 10 X 10 m were set out. Three quadrats of 2 X 2 m were randomly chosen in each plot, and within each quadrat, three trees (if present) were sampled at 3 different heights (TA: 0-50 cm, TB: 50 cm–1 m, TC: 1-

2 m). At each height on the tree (TA, TB, TC), 3 bryophyte samples of 10 X 5 cm (50 cm^2) were collected.

This size of sampling has been shown to well represent the diversity in a 10 X 10 m plot, as well as being a workable and convenient size in terms of species identification and time allocation.

Climatic data was recorded using MadgeTech (RHTemp1000) data loggers. Loggers were set up in May 2011, at each of the fourteen sites. Loggers were secured on a wooden pole 1 m above the ground. Temperatures and relative air humidity were measured at hourly intervals for 5 months, from May to September 2011. The data was collected using the MadgeTech 2.03 software.

Figure 1: Map of Africa, the Mascarene archipelago, and La Réunion

Species identification

The bryophyte samples were air-dried and stored in paper bags for later identification. Specimen identifications were undertaken by M. Chuah-Petiot (350 – 750 m samples), C. Ah-Peng and N. Wilding (950 -1350 m samples), J. Bardat (1550 – 1950 m samples) and T.A.J. Hedderson (2150 – 2750 m samples). Bryophyte nomenclature follows that of O'Shea (2006) for mosses, that of Wigginton (2009) for liverworts and hornworts and a checklist of bryophytes of the island (Ah-

Peng & Bardat 2005).

Selection and collection of functional trait data

The selection of liverwort functional traits analyzed in this study was based on their purported functional significance to the survival of the plant, often particularly in relation to water uptake. Descriptions of the traits and the reasons for their selection are described below:

a) *Lobules.* Many liverwort species have structures called lobules, which are sacs formed by an inrolled, rear leaf margin. These sacs are thought to play a role in holding external capillary water and preventing desiccation.

b) *Trigones.* These structures, unique to liverworts, are triangle-shaped thickenings of the cell wall occurring at the corner of the cell where it abuts against two other cells. Although the function of trigones is not well understood, it is speculated that they serve the same function as many cell wall thickenings in the leaf cells of vascular plants – water storage (Watson, 1967). This may be another adaptation of the plant to hold on to the extracellular capillary water.

c) *Ocelli* (*sin.* Ocellus). These specialized cells occur in the leaves of certain liverworts. They are enlarged cells that lack chloroplasts, but contain one or more unusually large oil bodies. Oil bodies are membrane-bound organelles that contain a diversity of ethereal terpenoid oils (Crandall-Stotler & Stotler, 2000). Although the functional significance of ocelli is unknown, the oil bodies are believed to provide protection from cold and/or UV radiation (Crandall-Stotler & Stotler, 2000).

d) *Secondary pigments.* Many liverworts biosynthesise secondary metabolites. These include terpenoids (the largest group of secondary metabolites in bryophytes) and aromatic compounds such as flavonoids (yellow- or orange-pigmented secondary metabolites). Again, the functions of these compounds are not well understood, but they are thought to play a role in providing anti-microbial protection, as well as protection from UV radiation (Xie & Lou, 2009).

e) *Leaf dissection.* There is much interspecific variation in the shape and form of liverwort leaves. They can be completely rounded and entire, or lobed. The degree of lobing varies from simple, bilobed leaves, to deeply dissected thread-like segments. Some leaves have

margins that are toothed. For this study, it was speculated that these bilobed, dissected and toothed leaves would be better able at retaining water, as the lobes or dissections could serve the same function of hyaline hairpoints in mosses – increasing the absorption of condensed water vapour.

f) *Papillae.* A number of liverwort leaves have papillae on their surfaces. These are minute, solid protuberances on cell surfaces and appear to aid water uptake by creating capillary channels on the leaf surface (Schofield, 1981).

g) *Size.* As mentioned previously, the surface-area to volume ratio is highly important for bryophytes, as this affects the rate at which they lose the extracellular water and dry out. Therefore, the stem diameter, leaf length, underleaf length, gametophyte width and length, and lobule length were selected for analysis.

Functional trait data was collected by P. Staménoff, S. Meek and C. Ah-Peng using a wide range of literature, as well as direct examination and measurement of herbarium and transect specimens. The presence of lobules, trigones, ocelli, papillae and secondary pigments (indicated by a yellowish, reddish or brownish colour in the plant) was recorded for each species. The leaf dissection (presence of bilobed, dissected or toothed leaves) was also recorded. Measurements of the gametophyte lengths, leaf lengths, underleaf lengths, stem diameters and lobule lengths were also collected. The lobule lengths were not analyzed directly, but divided by the associated leaf lengths in order to give a more accurate, relative size measurement and account for interspecific plant size variations. An elongation index was calculated by dividing the gametophyte length by the gametophyte width, in order to give another dimension of the plant size.

Size measurements were obtained with as the average of four measurements for each trait. When a size range was given in the literature (e.g. leaf length 0.5-1.5 mm), the midpoint was used as a single measurement for analysis.

Data analysis

In total, 156 liverwort species were analyzed in this project (see appendix). Ten thalloid liverworts were removed from the dataset for the multivariate analyses, as most of the traits involved structures that are not present on thalloid species (e.g. lobule and underleaf presence and length). Another six species were excluded from the multivariate analyses, as they were

missing one or two trait data. Due to the fact that only one liverwort species was found at 2550 m and 2750 m, these altitudes were excluded from analyses.

The percentage presence or the average size of a particular trait was obtained for each altitude. Both linear and non-linear (second-order polynomial) regressions were performed using a general regression model on STATISTICA 10 and presented graphically using Microsoft Excel 10. The function that best fit the data, having the highest R^2 and lowest p-value, was chosen between the two.

The daily mean, daily maximum and daily minimum values for temperature and humidity were plotted against altitude using Microsoft Excel 10. In order to quantify the extent of climatic variation at each altitude, the coefficient of variation was calculated for each site by dividing the standard deviation by the mean. This was calculated for temperature and humidity, and plotted against altitude. Mean, maximum and minimum temperatures were plotted over time for each altitude. Unfortunately, the sensor at 950 m was only set up at the end of May 2011, so one month of data are missing for this site.

Multivariate analyses were performed by JMP, version 8. A base 10 logarithm was used for gametophyte width and length, leaf length, elongation index and stem diameter to achieve a better approximation to normality. As mentioned above, species missing one or more functional trait data were excluded from the dataset. A Principal Component Analysis was performed to summarize patterns of covariation in functional traits. The first four components from the overall analysis accounted for more than 80% of the variation among species. Therefore, scores on these components were treated as variables in subsequent regression and cluster analyses. Cluster analyses were performed to identify groups of species exhibiting similar covariation in their functional traits. An Analysis of Variance was performed using STATISTICA 10 to test for significance between cluster groups with the mean altitudinal ranges of the species in the groups.

A Stepwise Multiple Regression analysis was performed on each functional trait, as well as the four principal components, with specific climatic variables using JMP 8. Climatic variables used in the analysis were mean, minimum and maximum temperature and humidity, as well as altitude. This analysis was done in order to establish which climatic variables contributed the most to the functional trait distribution, and to what degree.

RESULTS

Climatic

The mean temperature decreased steadily with altitude from May to September 2011, the lowest site having a mean temperature of 18.6 ℃, more than 10 ℃ warmer that the highest site (figure 2.a). Despite this average decrease however, the maximum temperatures did not follow this trend. The higher altitudes seemed to experience maximum temperatures similar to, and sometimes more than that of the lower sites, despite the mean and minimum temperatures decreasing. This is also shown by the coefficient of variation (CV), which increases with altitude (figure 2.b), indicating that the higher altitudes experienced much wider temperature ranges and greater temperature extremes than the lower sites. The exception here is 950 m which stands out among the lower altitudes as having a relatively high CV.

The mean relative humidity remained high from the lower sites up until 1750 m, after which it decreased steadily with altitude (figure 3.a). The maximum relative humidity did not vary with altitude, reaching 100% at all sites. As a result, the CV is lower for relative humidity than for temperature, but it still shows the same pattern of increasing with altitude (figure 3.b). Again, the exception was 950 m, which experienced a much lower relative humidity compared to the adjacent altitudes.

Despite the decrease in temperature and humidity up the altitudinal gradient, many altitudes experienced much variation in temperature and humidity on a daily basis over the 5 month period (Figures 1-14, appendix). Up to an altitude of around 1950 m, relative humidity stayed consistently high, with almost all maximum values reaching 100 %. Minimum values did not seem to deviate greatly until 1950 m, after which the humidity levels reached very low points, the lowest being 2 % (2750 m).

Similar trends occurred for the temperature data, with the lowest altitudes showing little variation in temperature, and the highest altitudes showing greater variation, reaching temperatures from below 0 ˚C to 23 ˚C. It is interesting to note that a drop in relative humidity at a site can almost always be associated with a noticeable increase in temperature at the same time. This can be easily seen in the daily mean values from 1950 m upwards.

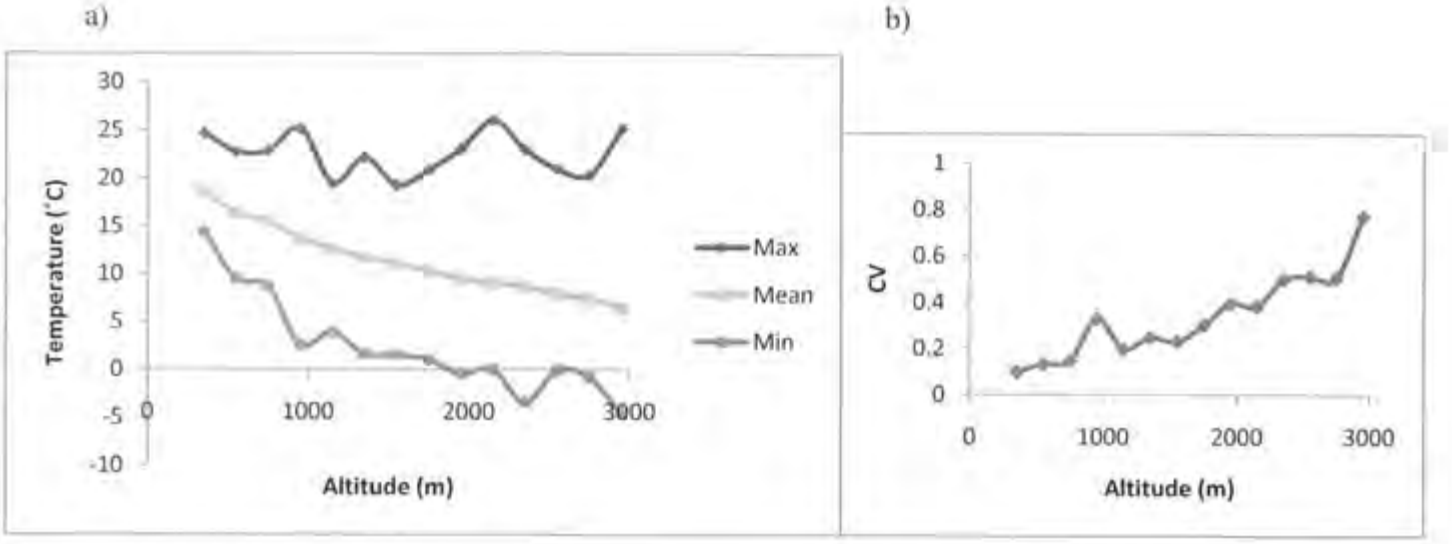


Figure 2: a) Mean, maximum and minimum temperatures and (b) the coefficient of variation of temperature from May – September 2011 at each altitude.

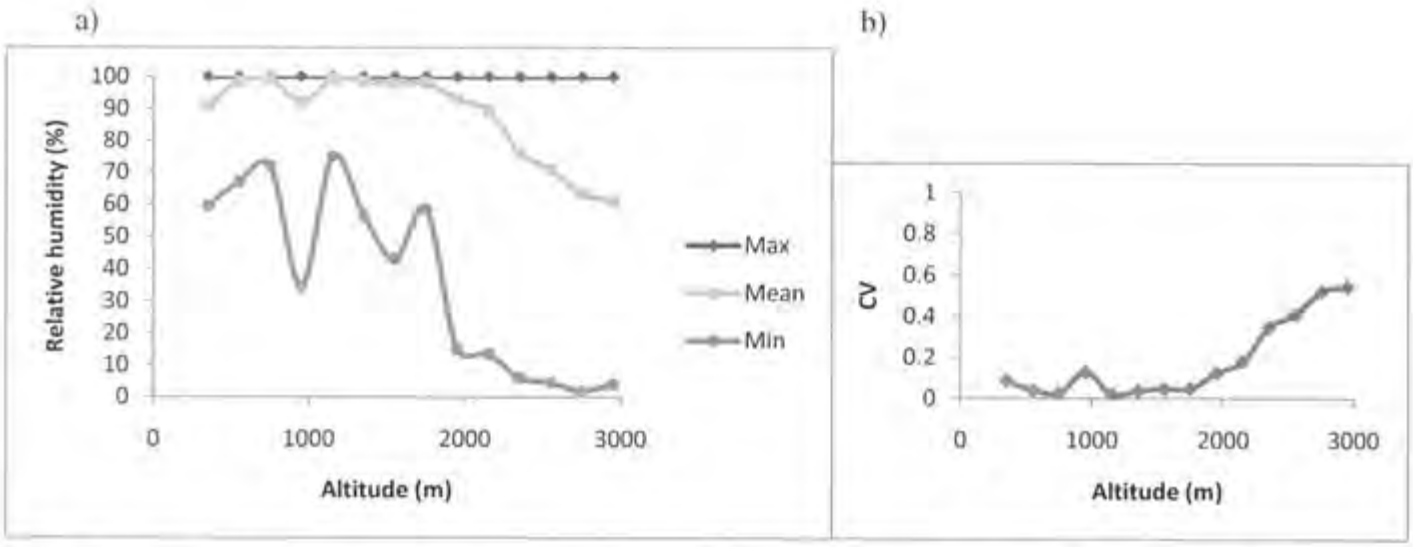


Figure 3: a) Mean, maximum and minimum relative humidity and (b) the coefficient of variation of relative humidity from May – September 2011 at each altitude.

Functional traits

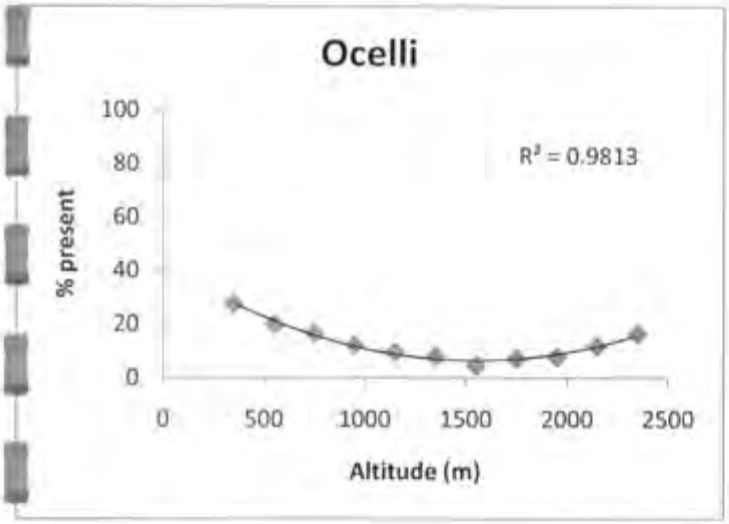
Of the thirteen functional traits analyzed, ten were found to have significant regressions on altitude (figure 4, Table 1 in appendix), with altitude accounting for 48-98% of the variation in these.

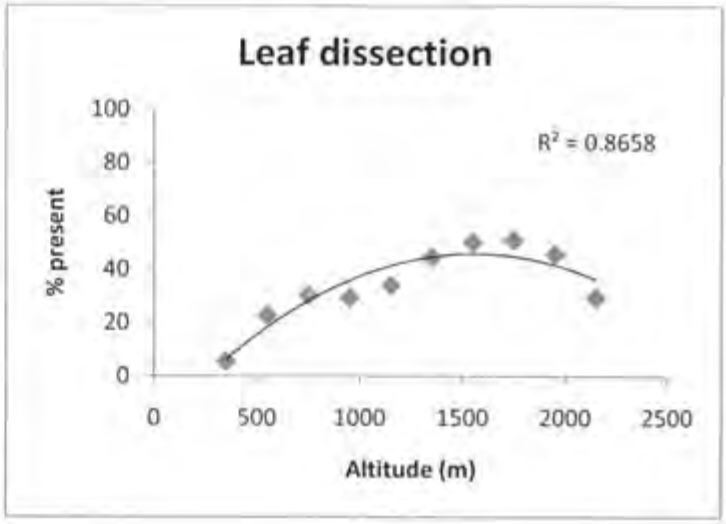
The most striking relationship was the proportion of species with ocelli ($R^2 = 0.98$, $p < 0.0001$). This percentage s is highest (28%) at the lowest altitude, decreasing to 5% at 1500 m, and then increasing again towards the highest altitudes. The percentage of species that had dissected, bilobed or toothed leaves showed an opposite trend to this, with the highest number of species occurring at the mid-elevation of 1500 m, again highly significant with $R^2 = 0.87$.

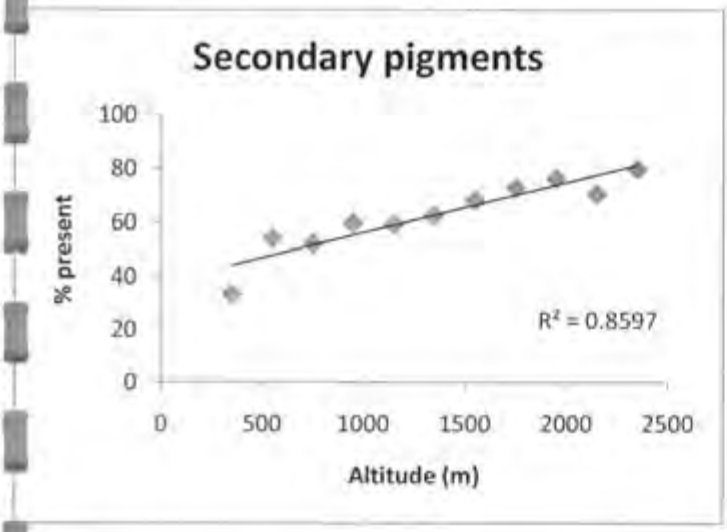
The percentage of liverwort species with secondary pigments increased significantly with altitude ($R^2 = 0.86$, $p = 0.0004$). The same trend was seen for the presence of trigones in the leaves, although the relationship was not as strong ($R^2 = 0.65$, $p = 0.005$). The presence of lobules showed the same non-linear regression as the ocelli, with the greatest percentage of species with lobules occurring at the lowest and highest altitudes.

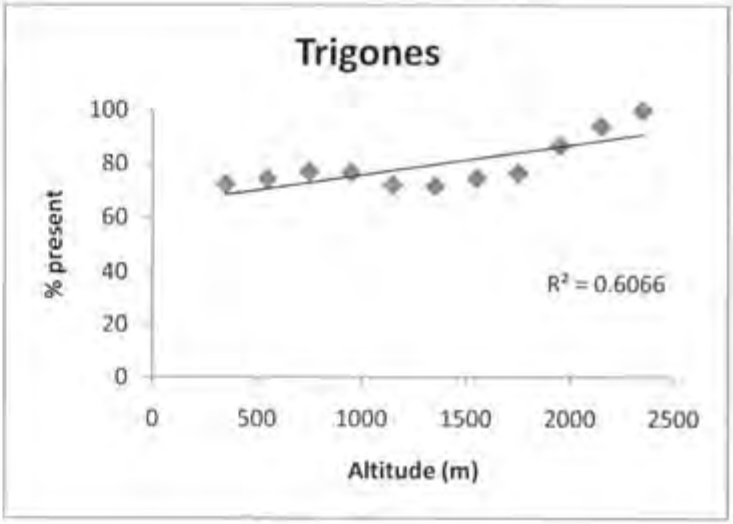
Three of the size measurements, leaf length, underleaf length and stem diameter, showed very similar, non-linear trends, the strongest and most significant relationship being the underleaf lengths ($R^2 = 0.80$, $p = 0.001$). The sizes of the leaves, underleaves and stem diameters were lowest at the lowest and highest altitudes, reaching a peak in the mid-altitudinal elevations.

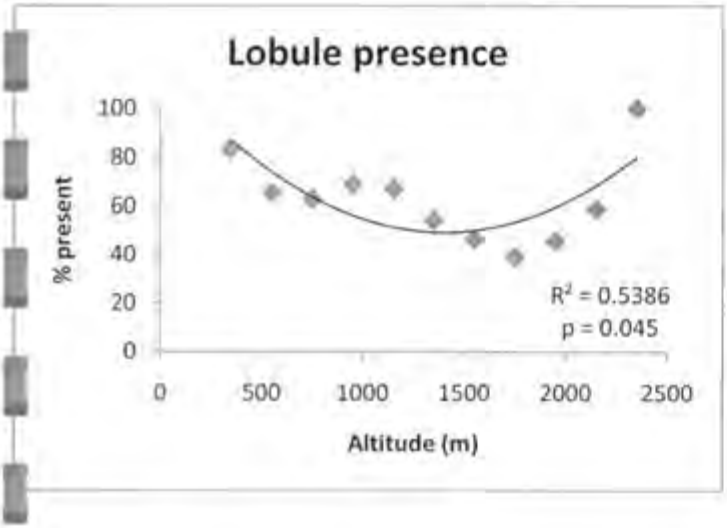
Gametophyte lengths decreased significantly with increasing elevation, although the relationship was not very strong ($R^2 = 0.49$, $p = 0.017$). The opposite trend was seen for lobule lengths, which increased with increasing altitude.

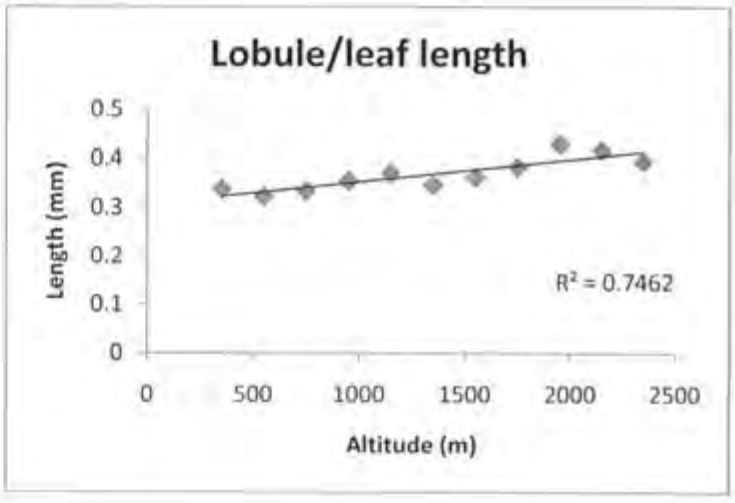

Ocelli
100
80
60
40
20
0
% present
$R^2 = 0.9813$
0
500
1000
1500
2000
2500
Altitude (m)

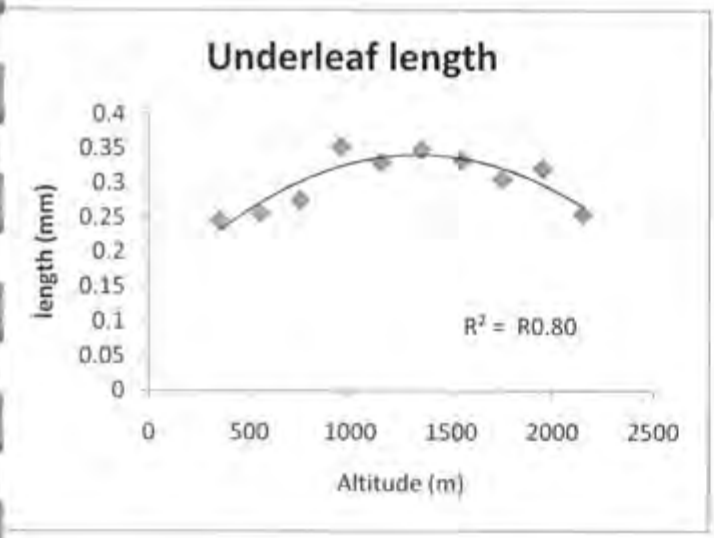

Leaf dissection
100
80
60
40
20
0
% present
$R^2 = 0.8658$
0
500
1000
1500
2000
2500
Altitude (m)

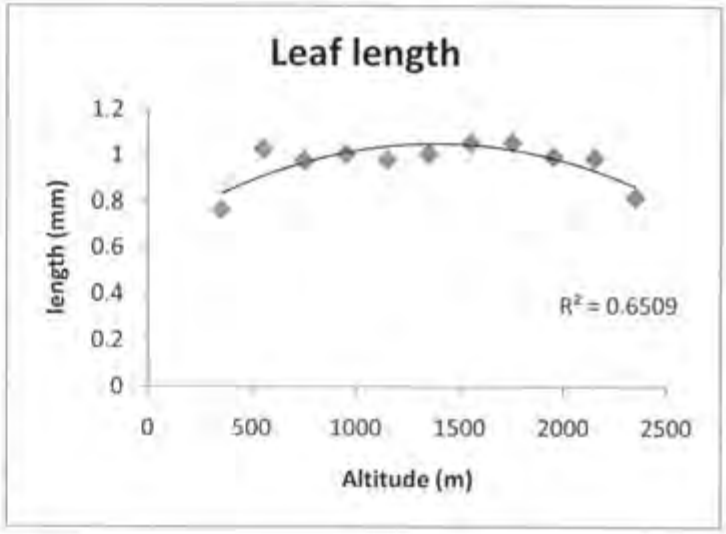

Secondary pigments
100
80
60
40
20
0
% present
$R^2 = 0.8597$
0
500
1000
1500
2000
2500
Altitude (m)

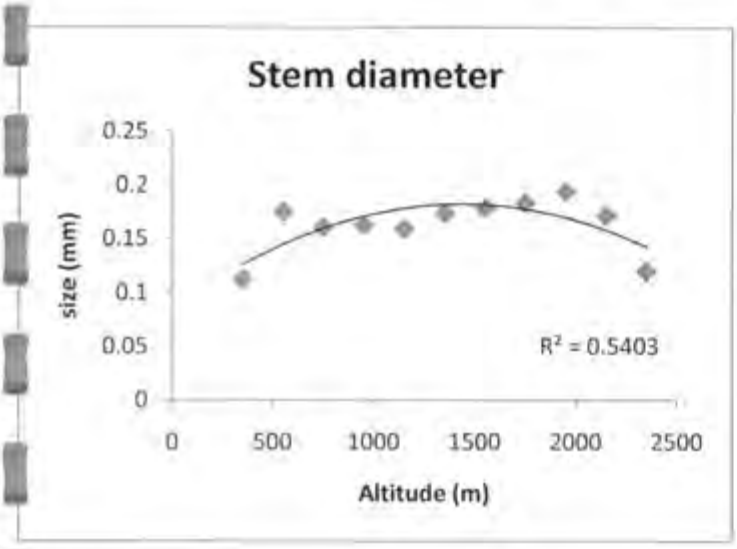

Trigones
100
80
60
40
20
0
% present
$R^2 = 0.6066$
0
500
1000
1500
2000
2500
Altitude (m)


Lobule presence
100
80
60
40
20
0
% present
$R^2 = 0.5386$
p = 0.045
0
500
1000
1500
2000
2500
Altitude (m)


Lobule/leaf length
0.5
0.4
0.3
0.2
0.1
0
Length (mm)
$R^2 = 0.7462$
0
500
1000
1500
2000
2500
Altitude (m)







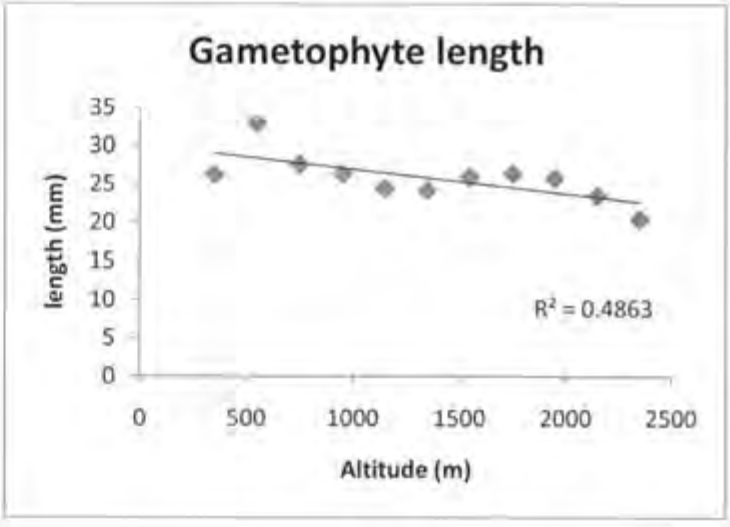


Figure 4: Regressions of functional traits on altitude

Multivariate analyses

The first four principal components account for ca 82.39 % of the covariation among the 13 investigated functional traits. The eigenvectors of these four components are displayed in table 4.

Table 3: Eigenvectors and percentages of the first four principal components

	1	2	3	4
Log Leaf length	0.2903	-0.1296	-0.3743	-0.0636
Log Gametophyte length	0.5852	-0.1413	0.27186	-0.3344
Log Gametophyte width	0.28853	-0.1166	-0.3991	-0.1459
Log Elongation index	0.30276	-0.0235	0.66734	-0.1871
Log Stem Diameter	0.35395	-0.0336	-0.277	-0.1169
Lobule Length	0.01923	-0.015	0.01827	0.10413
Lobule:leaf length	-0.1277	-0.0164	0.14672	0.15959
Trigone	0.31178	-0.4454	0.09391	0.81709
Ocelli	-0.136	0.09366	0.26963	0.04158
Secondary pigments	0.37508	0.86043	-0.0361	0.32938
Eigen-value	0.4027	0.2271	0.2062	0.1461
Percentage	33.782	19.049	17.3	12.255
Cumulative percentage	33.782	52.83	70.13	82.386

Principal Component one, which accounted for 33.78 % of the variability, describes a gradient from plants with long leaves and stems, large stem diameters and a high elongation index (longer plants) to those with the opposite suite of traits. Interestingly, the relative lobule lengths (lobule:leaf length ratio) tended to be smaller on the larger plants, and they tended to have secondary pigments, as well as trigones, but tended not to have ocelli.

Variables with high loadings on Principal Component two (19.05% of covariance) are trigone presence and production of secondary pigments. Size variables also have relatively high negative variables on this axis.

The plants in principal component three had high elongation indices, meaning that they were long and thin, and had small stem diameters. These plants tended to have ocelli. Principal

component four consisted of plants which were small, and not long. They tended to have trigones.

Each of the four principal components was found to have significant regressions with altitude (figure 5). Component 1 and 2 both had their lowest scores at the lowest altitudes, increasing with altitude before dropping again at the highest altitudes. Principal component 3 had a very strong non-linear relationship, with the highest scores at the lowest and highest altitudes. Principal component 4 had a strongly significant, linear increase with altitude.

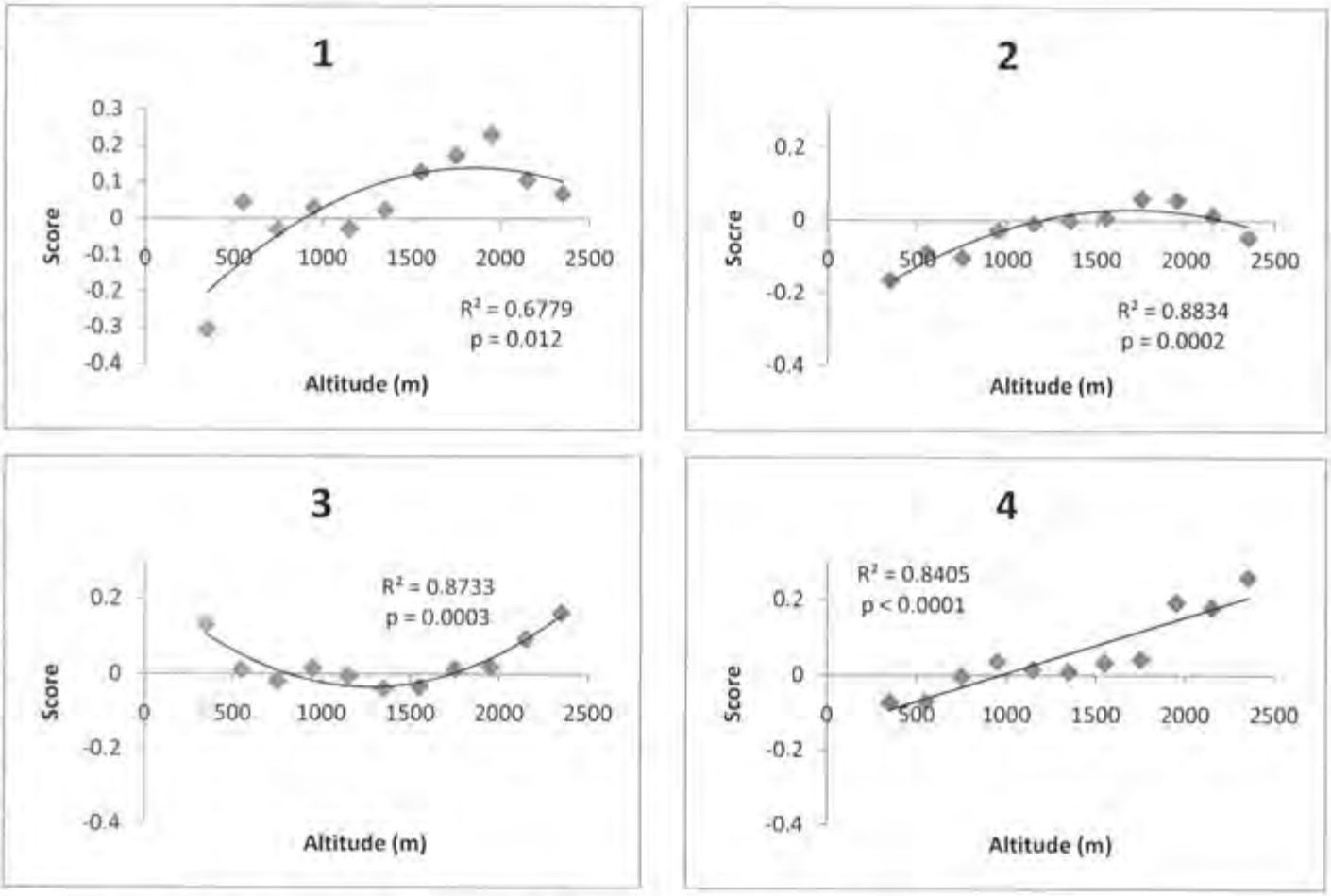


Figure 5: Scatterplots and regressions of principal components with altitude

Cluster analyses separated species into seven groups based on patterns of covariation among functional traits (figure 6). The long branch lengths and high degree of homogeneity within clusters is evidence that the groups are distinct from each other.

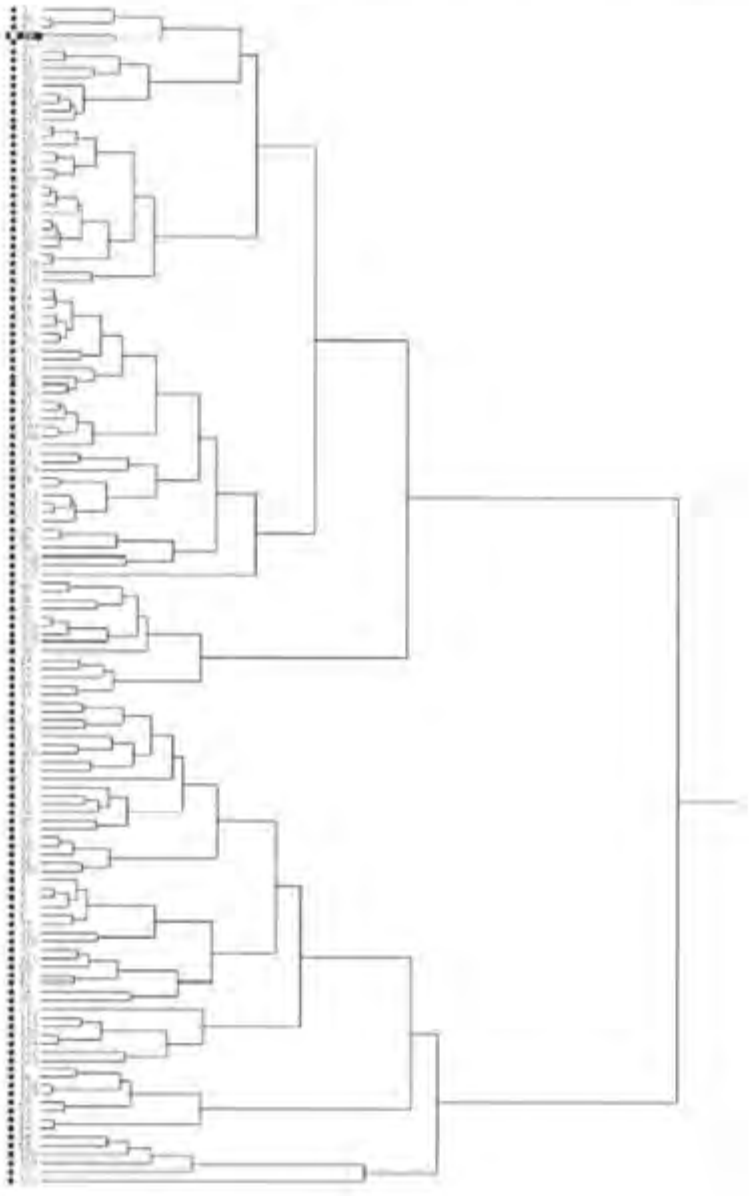


Figure 6: Cluster diagram for liverwort functional traits

A summary of the functional traits in each cluster is presented below (table 4). Values are given as the average of all values for that cluster. Cluster 6 was removed as it only consisted of one species.

Table 4: Summary of functional traits for the six clusters

		1	2	3	4	5	7
Size (mm)	Leaf	0.57	1.35	1.46	0.45	0.57	0.91
	Gametophyte	13.04	29.31	104.00	14.94	15.80	24.43
	E.I.	13.52	13.06	86.60	29.00	17.24	22.00
	Stem	0.08	0.24	0.27	0.10	0.06	0.16
	Underleaf	0.19	0.26	0.86	0.08	0.19	0.28
	Lobule:leaf	0.40	0.00	0.09	0.00	0.34	0.32
% Present	Lobules	100	0	40	0	100	94.4
	Leaf dissection	3.0	67.4	80	100	14.3	8.3
	Trigones	66.7	81.4	100	0	64.3	94.4
	Ocelli	0	0	0	0	100	5.6
	Papillae	15.2	4.7	20	100	7.1	0
	Underleaf	72.7	69.8	100	87.5	100	80.6
	Sec. pigments	21.2	65.1	100	50	57.1	88.9

Species grouped into cluster 1 were small in size, all having lobules present on their leaves. Despite the small average size of the plants, the average lobule size was biggest of all the clusters. Species in cluster 2 were larger in size, had no lobules, and 81.4 % of them had trigones present. Around 65% of them also had underleaves and secondary pigments. Cluster 3 consisted of the longest species (mean of 104 mm) but were also very thin (E.I of 86.6). All of these large plants had trigones, underleaves and secondary pigments, and 80% of them had dissected leaves. Cluster 4 consisted of small species that all had dissected leaves and papillae. They did not have lobules, trigones or ocelli, but 87.5% of them had underleaves. Cluster 5 consisted of species that all contained lobules, ocelli and underleaves. Despite the small size of these plants, the average lobule size was relatively bigger than the other clusters. Cluster 7 consisted of a large percentage of species all having lobules, trigones, underleaves and secondary pigments.

A one-way ANOVA test compared the mean altitudinal ranges of the clusters and found them to be significantly different (df = 5, 131; F = 2.354; p = 0.044). Figure 7 shows the mean altitudinal range and variance for each cluster. Cluster 2 had the highest mean altitudinal range as well as the smallest variance. Cluster 5 consisted of species that had lower altitudinal ranges.

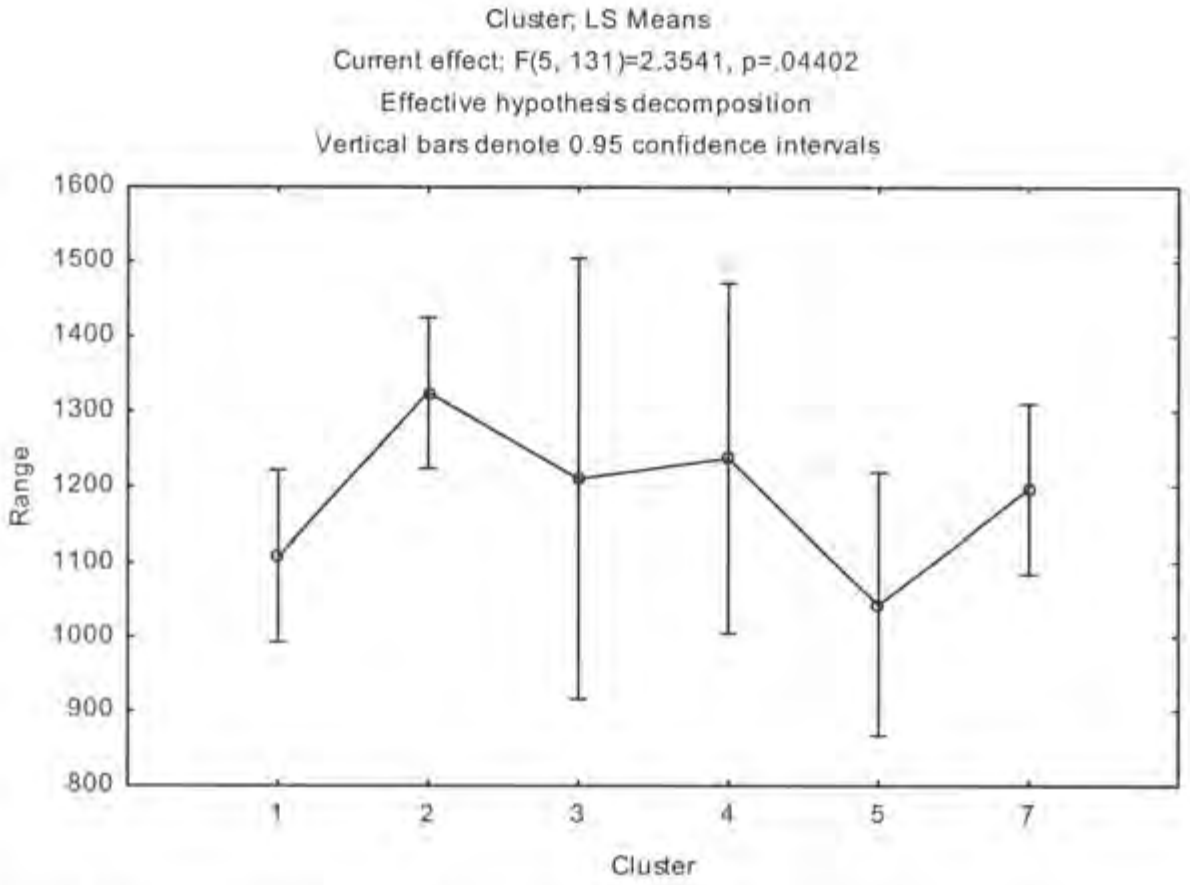


Figure 7: Mean altitudinal range and variance for the six clusters

The Stepwise Multiple Regression analysis showed that a number of functional traits have significant relationship with various climatic variables. These relationships and their significance are shown in table 5. The positive/negative sign in the slope column gives the direction of the slope and relationship.

Table 5: Stepwise Multiple Regression analyses on functional traits and principal components on altitude and climatic variables.

Functional trait	Climatic variable	R^2	F	p	slope
Ocelli	Daily min temperature	0.54	169.122	0.010	+
	Daily mean humidity	0.96	80.525	< 0.001	-
Trigones	Daily min humidity	0.75	0.069	0.001	+
Lobules	Daily mean humidity	0.50	51.668	0.016	-
	Daily min humidity	0.87	9.604	0.001	+
Sec. pigments	Daily mean temperature	0.92	104.581	< 0.001	-
Leaf dissection	Daily mean humidity	0.36	26.225	0.001	-
Lobule:leaf length	Altitude	0.75	26.457	0.001	+
Underleaf length	Altitude	0.43	19.913	0.005	-
Stem diameter	Daily mean humidity	0.36	54.448	0.050	+
	Daily min humidity	0.87	12.806	0.001	-
Leaf length	Daily mean humidity	0.44	34.307	0.025	+
	Daily min temperature	0.83	17.901	0.003	-
Gam. length	Altitude	0.49	3.569	0.017	-
PC 1	Average daily temp	0.64	7.364	0.003	-
PC 2	Average daily temp	0.72	83.565	0.001	-
	Daily mean humidity	0.91	18.292	0.003	+
PC 3	Daily mean humidity	0.76	126.963	0.001	-
	Daily min temperature	0.89	14.97	0.015	+
	Daily mean temperature	0.95	8.317	0.024	-
PC 4	Altitude	0.84	13.526	< 0.001	+
	Daily min humidity	0.92	8.843	0.018	-

DISCUSSION

The results of this study provide objective evidence for the existence of patterns in functional traits of corticolous liverwort species along a tropical altitudinal gradient. Groups of species were defined by these patterns, and were related to altitudinal changes in climatic conditions, specifically temperature and humidity. Therefore, it would seem that these patterns of traits form functional groups that are biologically meaningful, and whose distributions are related to the environmental conditions of that habitat.

According to Frahm and Gradstein (1991), the most important climatic factors used in studies of altitudinal vegetation changes are measures of temperature and humidity. Relative humidity provides an indication of the precipitation and amount of potential evapotranspiration in a particular habitat. The overall climatic changes that occurred along the altitudinal gradient in this study closely mirror those found in previous studies and sites (Frahm & Gradstein, 1991; Kluge & Kessler, 2011). Aside from the similar trends, it is interesting to note the wide range of conditions experienced at some of the sites, sometimes reaching temperatures below 0 ℃ at high altitudes. One altitude that stood out among the lower sites in terms of its climatic extremes was 950 m. The marshy, wet-thicket vegetation at this site was unique compared to others along the gradient, consisting of many endemic species to the island and the archipelago (>50 % of endemic species form this habitat). It was also very distinct from the lowland forest vegetation below, and the rainforest vegetation above; the scarcity of tall trees and canopy provided little shade and protection. The gradient of environmental conditions found along this altitudinal transect, and the overall decrease of average temperature and humidity, may well explain the distribution of functional traits found in this study.

When analyzed individually, ten of the thirteen functional traits used in this study were found to have a significant relationship with altitude. These relationships were either linear or non-linear, depending on the trait, and all varied in terms of the strength and significance of the relationship. Although no study has yet related changes of bryophyte functional traits with altitude, patterns of bryophyte species turnover and distribution are known to be associated with changes in altitude,

and bryophytes have even been proposed as useful tools for altitudinal zonation of tropical rainforests (Frahm, 1990; Frahm & Gradstein, 1991).

The multivariate analysis summarized patterns of trait covariation into principal components, the first four of which were found to have a significant relationship with altitude. From the regressions of functional traits as well as the principal components, certain patterns of trait distribution with altitude can be identified. For example, the relationship of trigone and secondary pigment presence, both increasing linearly with the altitude, have the same linear trend as principal component 4 which weights these traits heavily. These relationships provide additional evidence for the influence and importance of functional traits on species distributions along an altitudinal gradient. The cluster analyses grouped species into communities according to similarities in functional traits. The six distinct, cluster groups showed a significant difference in their altitudinal range, thereby supporting the hypothesis that particular functional traits are associated with species occurring in specific distribution ranges.

The Multiple Regression results showed that functional trait distributions were not only related to altitude, but also to changes in the separate climatic variables, sometimes very strongly so. It would appear that a single functional trait can be influenced by more than one climatic variable (temperature and humidity). For example, ocelli presence has a positive relationship with temperature, and an equally strong negative relationship with humidity. Different extremes of a climatic variable (min or max) can also significantly affect the distributions. These relationships provide some explanations behind the patterns of species distribution observed along the altitudinal gradient – with changes in climatic conditions determining the functional traits best suited for water uptake and storage in those conditions.

The number of the traits and trait combinations show relationships with climatic variables that have been supported by the literature. For example, PC 4 increased linearly with altitude and had a positive, linear relationship with minimum humidity. PC 4 consists of a gradient from small plant sizes and high trigone presence to plants with the opposite traits on the other end. The relationship with humidity could suggest that large plants, with a larger surface-area to volume ratio, are less dependent on trigones for water storage and retention, as their larger size buffers them from rapid desiccation. This trend would therefore support the speculation that trigones are in fact traits that serve the plant in water storage (Watson, 1967).

Another interesting linear relationship was that of secondary pigments with altitude. A study done by Hooijmaijers and Gould (2007) showed that gametophytes of a single liverwort species, *Jamesoniella colorata*, displayed different colour pigments depending on whether the plant was placed in an exposed, or shaded habitat. They found that the red gametophytes had a higher potential for mitigating the damaging effects of high irradiance than the green gametophytes. Perhaps the decrease in shade cover and canopy with the higher altitudes accounted for this trend.

In the last two decades, functional trait research has become much more focused on the importance of functional group richness as a measure of biodiversity, with species richness representing only one level of biological organization (Hillebrand & Matthiessen, 2009). Functional traits are increasingly being used to understand ecological processes, and to assist ecology in becoming a more predictive science. This study gives evidence of another level of biological organization in bryophyte communities in response to altitude, temperature and humidity.

Bryophytes are an important group of plants in these tropical rainforest, with a high diversity, abundance and occupy a large variety of microhabitats (Frahm & Gradstein, 1991). The biological, functional trait organization of bryophyte species is therefore important to understand, as it affects the processes involved in the functioning of ecosystems and the communities to which they belong (Chapin *et al.*, 2001). As described by Cianciaruso *et al.*, (2009), functional traits affect and control the competitive ability (e.g. the ability to invade) and coexistence of species (Richards *et al.*, 2006), and their ability to withstand particular disturbances of an environment. Functional traits also influence the contribution of a species to a community functioning by affecting plant productivity (Cianciaruso *et al.*, 2009).

The influence of species diversity on fluxes of energy and matter which affect ecosystem functioning are processes that are important to understand, as they control the abundance, distribution and biomass of organisms around the world (Cardinale *et al.*, 2006). Research has shown that greater diversity in plant functional traits allows for greater access to ecosystem resources, such as nutrients, water, pollinators or fungal symbionts (Tilman, 1999). Therefore, plant diversity is directly proportional to community productivity (Cadotte *et al.*, 2009) and measuring functional diversity in relation to limiting resources is believed to be a good predictor

of plant productivity. Understanding these processes is necessary in today's world, where predicting the impacts of global change on ecosystem functioning is crucial.

This study is a pioneering one, and can be furthered in many aspects. Experimental investigation, focussing particularly on intraspecific trait variation, will give a greater understanding of specific traits and their associated roles and functional significance. The co-adaption of traits can also be further explored. Although there are a number of seemingly independent traits in this study that are closely associated with each other (e.g. trigone and secondary pigment presence), the mechanisms behind this are not explained here. The extent to which the association between functional traits and environmental correlates signifies co-adaptation requires investigation, as well as whether single traits are strictly adaptive, or occur as a result of common ancestry (Hedderson & Longton, 1995).

A phylogenetic approach would contribute greatly to understanding the distribution of liverwort functional traits with altitude, and to what extent this may be controlled by abiotic factors. Hedderson and Longton (1996) discussed the taxonomic effects and restrictions on variability in water relations and life history traits of bryophytes. They acknowledged that the joint evolution of traits would need to be tested using explicit, independent phylogenetic hypotheses in order to understand the coevolution of traits into adaptive combinations.

Although this study has probably raised more questions than answers, it has shown that strong patterns of species functional traits occur along an altitudinal gradient. This study has the potential to contribute to the direct, predictive application of functional trait ecology. Not only can these plants serve as indicators of climate change along altitudinal and latitudinal gradients, but the consequences of their changing biodiversity in ecosystems can be better understood, as well as the ecosystems to which they belong.

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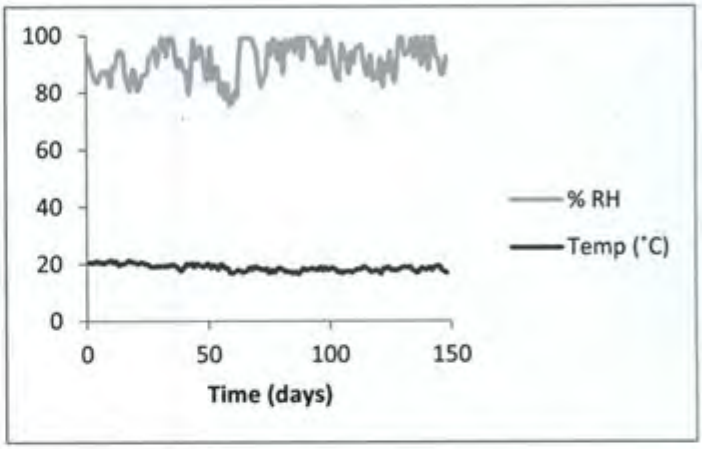
APPENDIX

350m

a)

b)



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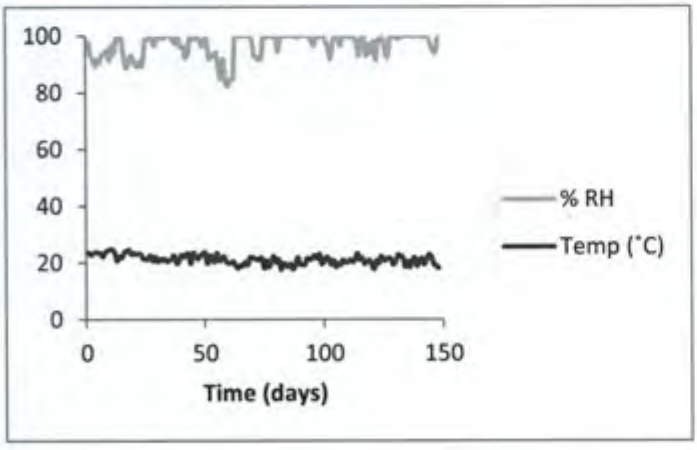

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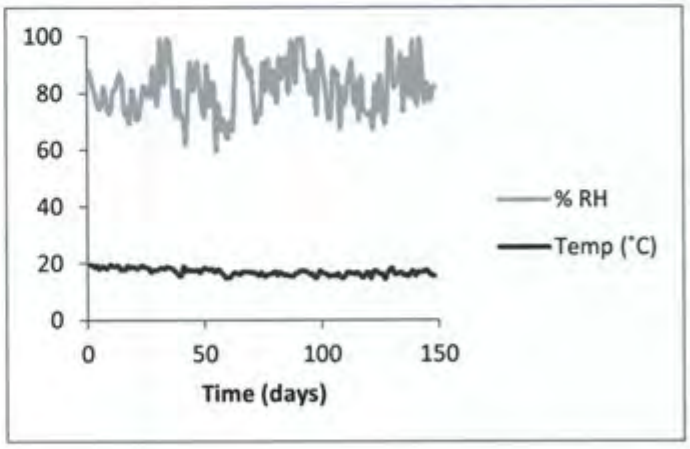
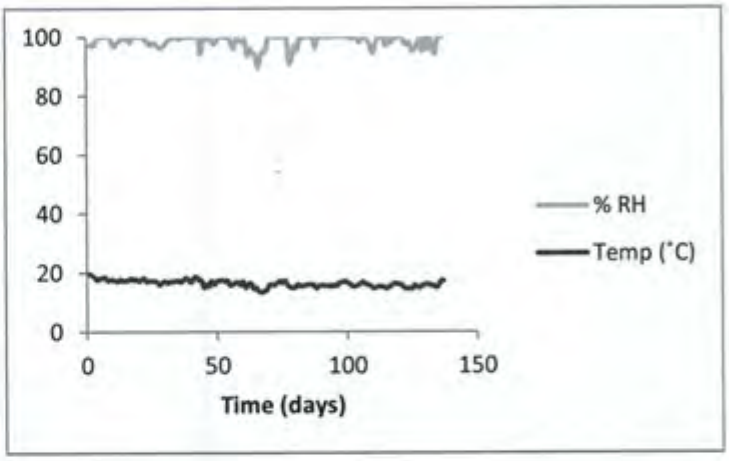


Figure 1: a) Lowland rainforest at the 350 m site. Temperature and relative humidity data over the 5 month period at 350 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity. d) Daily minimum temperature and humidity.

550 m

a)

b)



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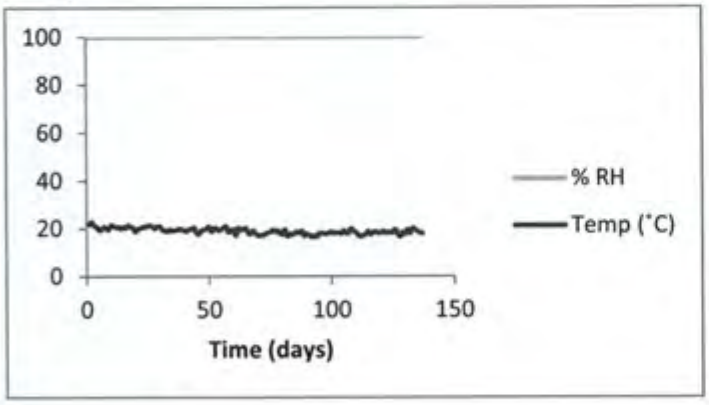

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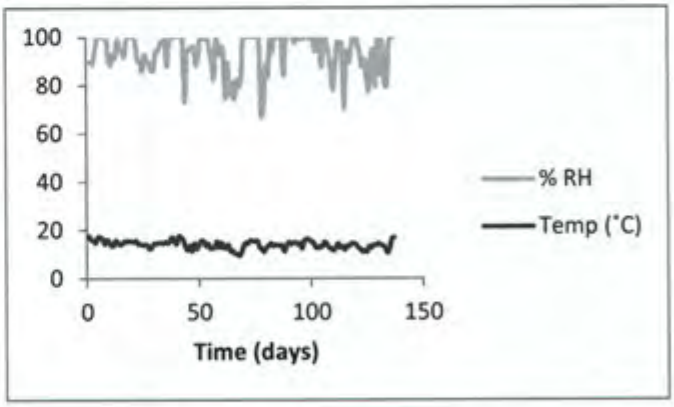
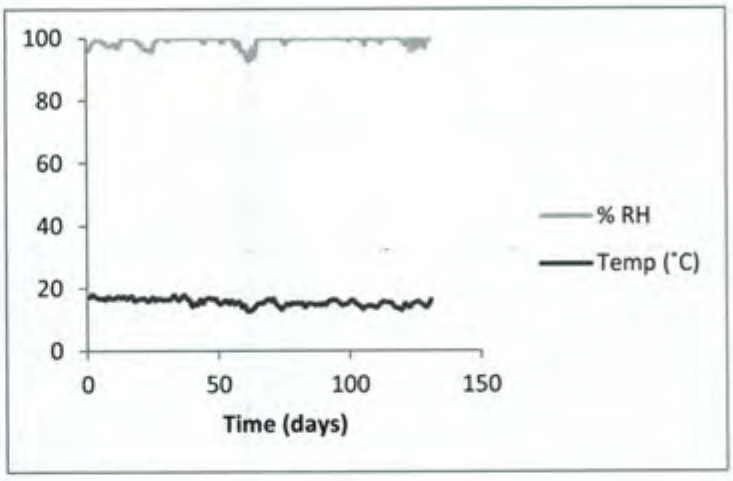


Figure 2: a) Lowland rainforest at the 550 m site. Temperature and relative humidity data over the 5 month period at 550 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity. d) Daily minimum temperature and humidity.

750 m

a)

b)



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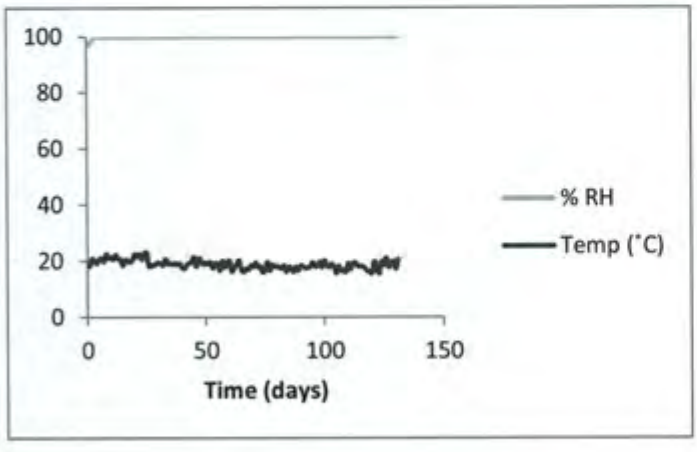

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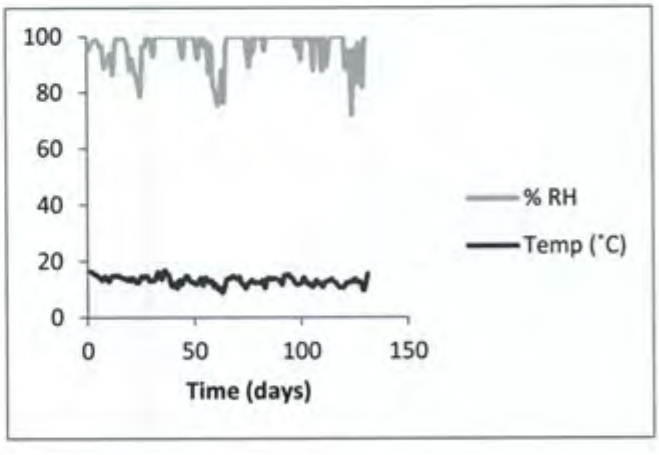
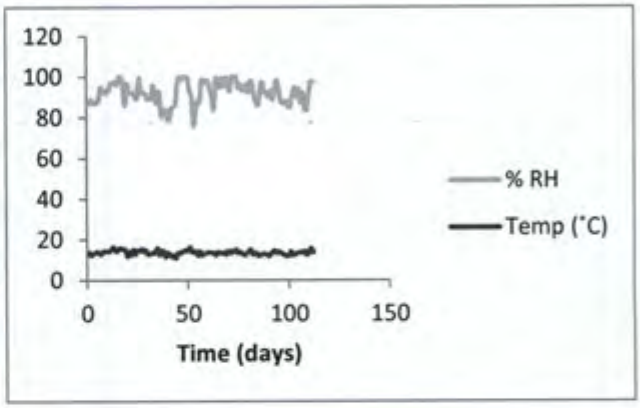


Figure 3: a) Lowland rainforest at the 750 m site. Temperature and relative humidity data over the 5 month period at 750 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity. d) Daily minimum temperature and humidity.

950 m

a)

b)



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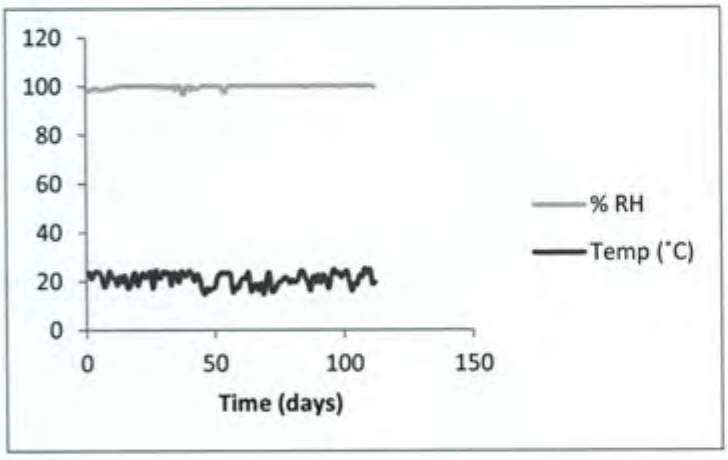

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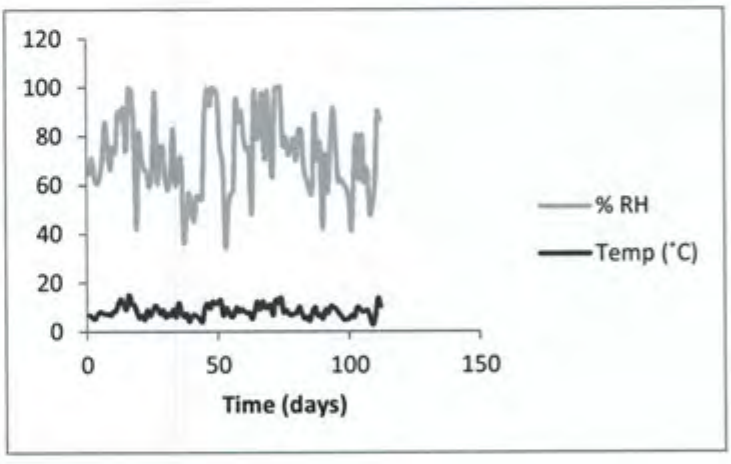


Figure 4: a) Wet thicket at the 950 m site. Temperature and relative humidity data over the 5 month period at 950 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

1150 m

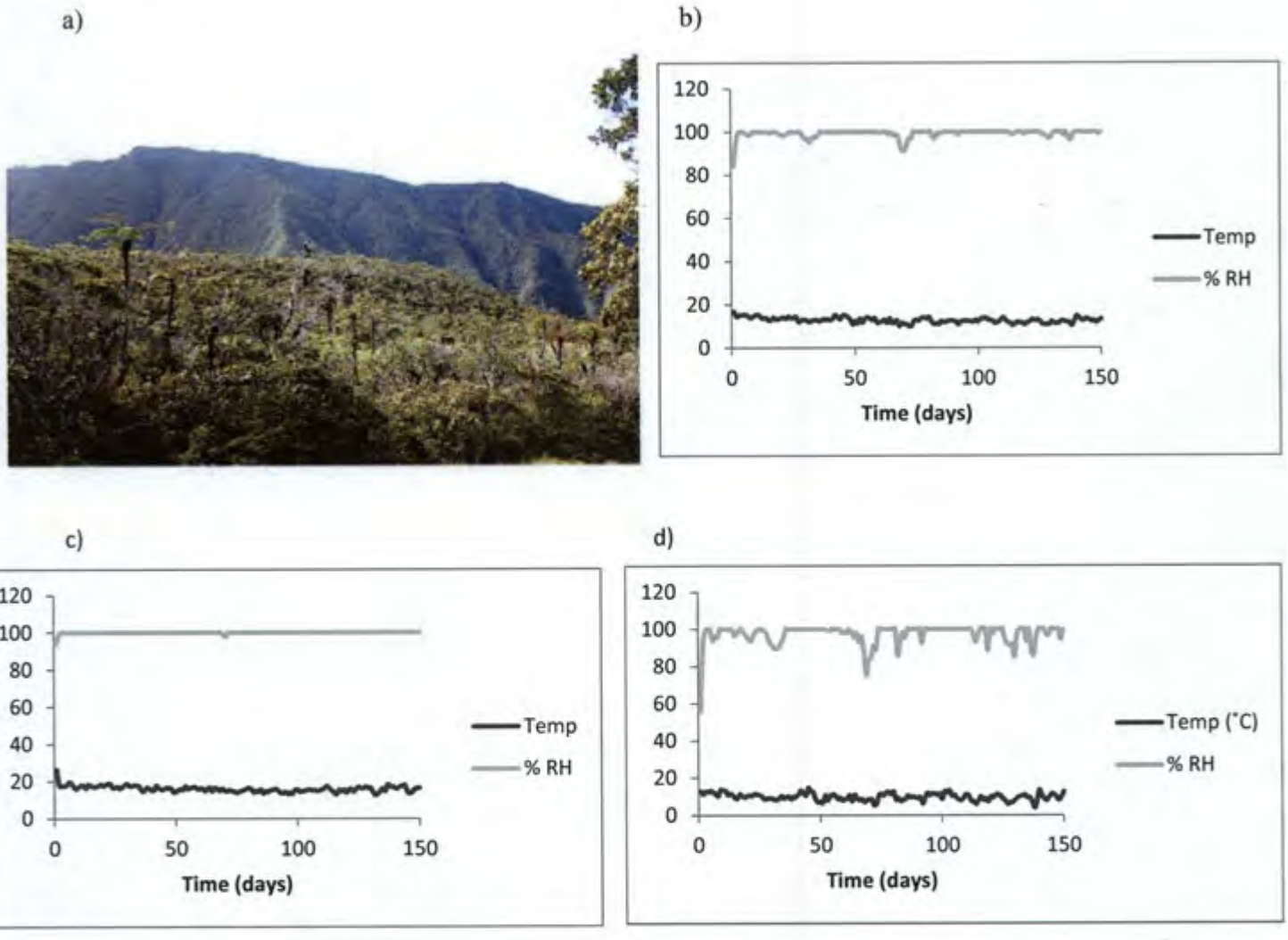


Figure 5: a) Submountain windward forest at the 1150 m site. Temperature and relative humidity data over the 5 month period at 1150 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

1350 m

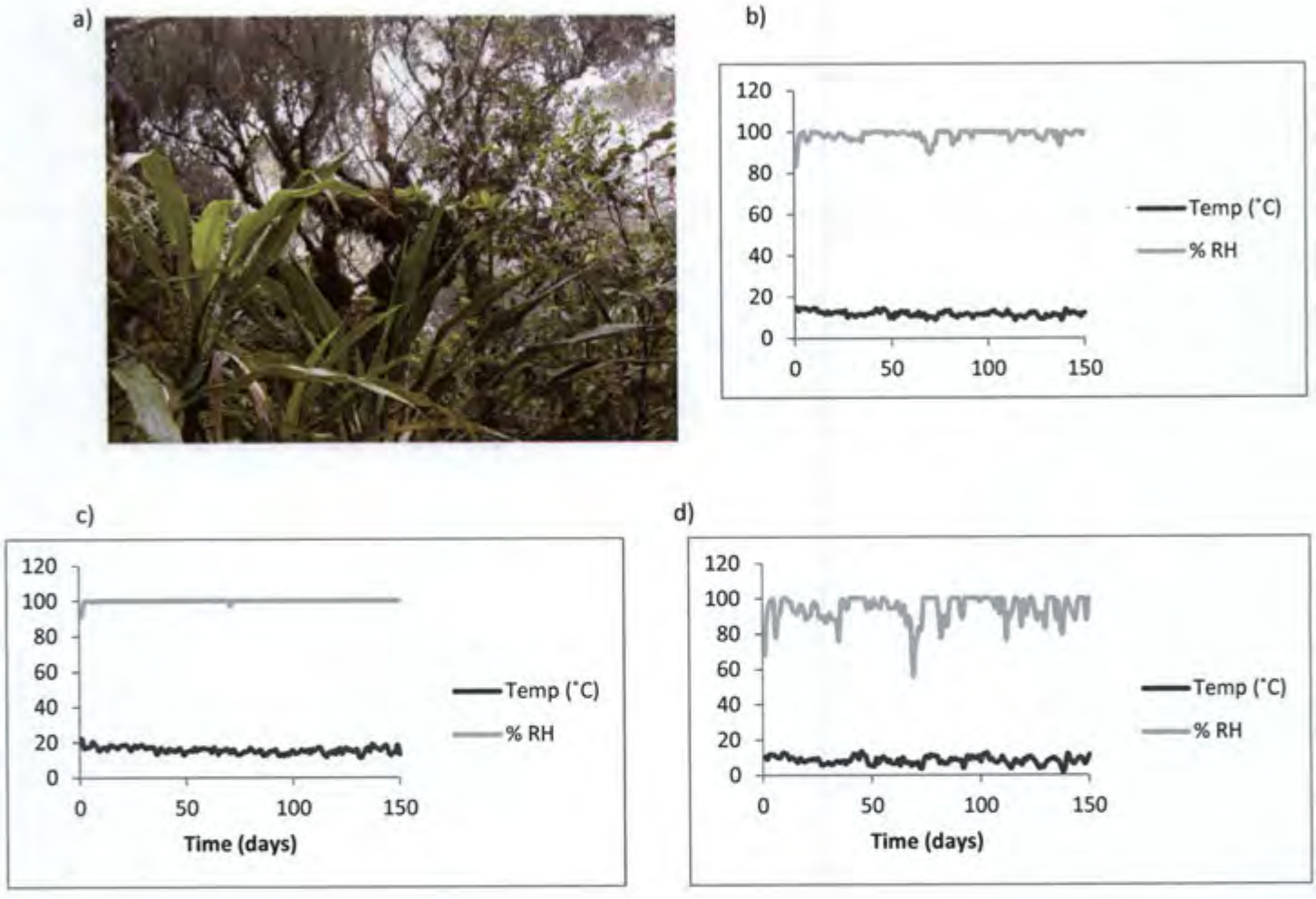
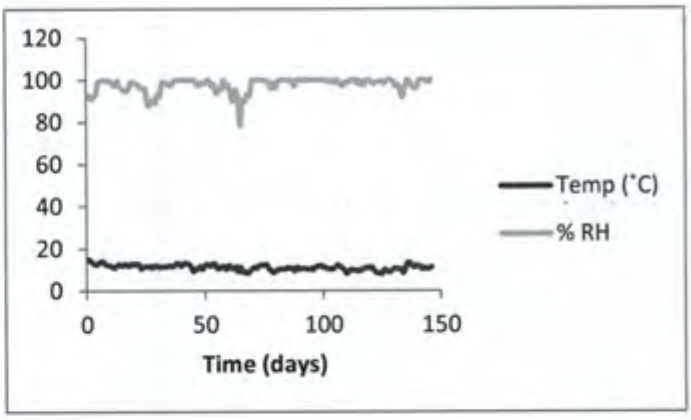


Figure 6: a) Submountain windward forest at the 1350 m site. Temperature and relative humidity data over the 5 month period at 1350 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

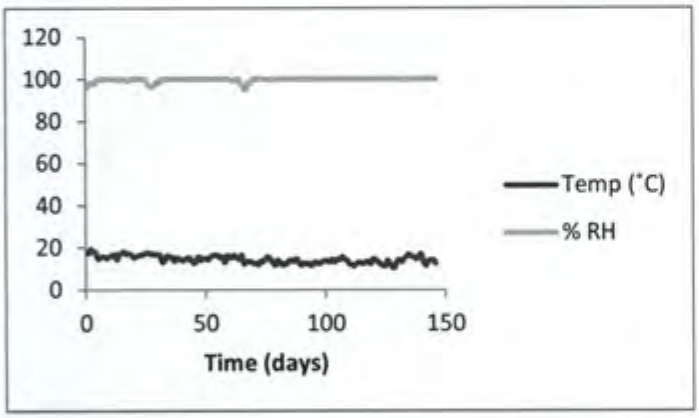
1550 m

a)

b)



c)



d)

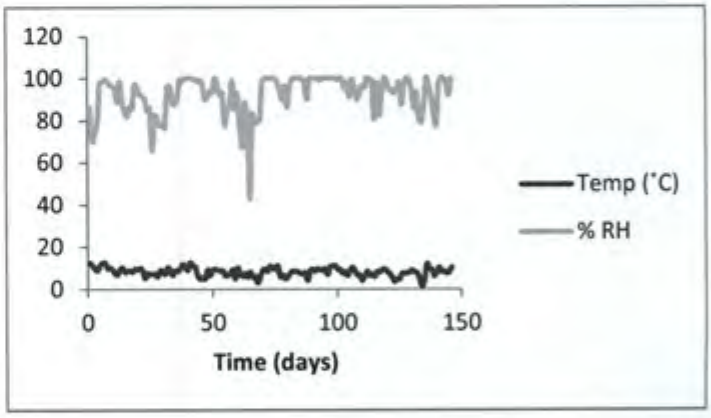
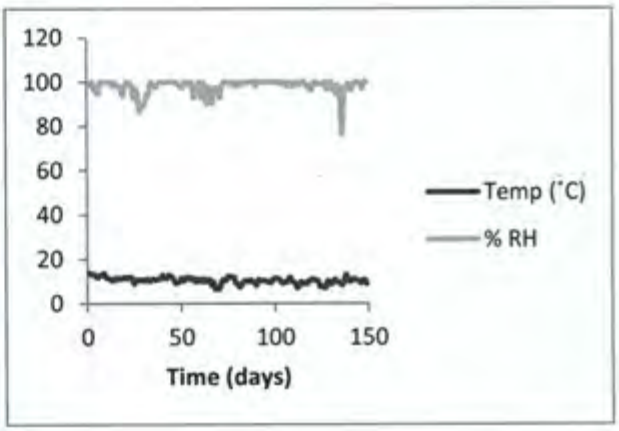


Figure 7: a) *Accacia heterophylla* mountain forest at the 1550 m site. Temperature and relative humidity data over the 5 month period at 1550 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

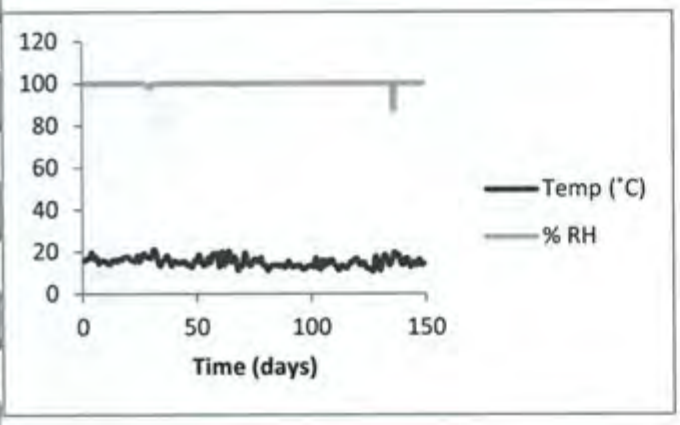
1750 m

a)

b)



c)



d)

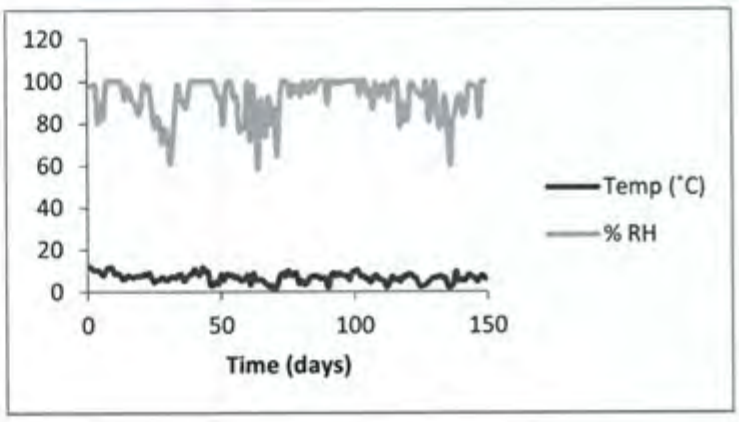
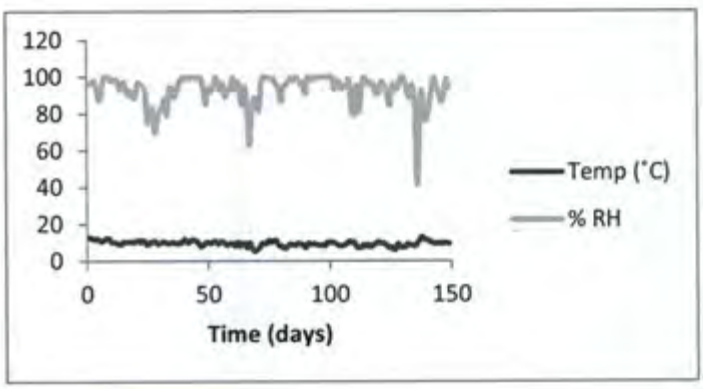


Figure 8: a) Mountain windward forest at the 1750 m site. Temperature and relative humidity data over the 5 month period at 1750 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

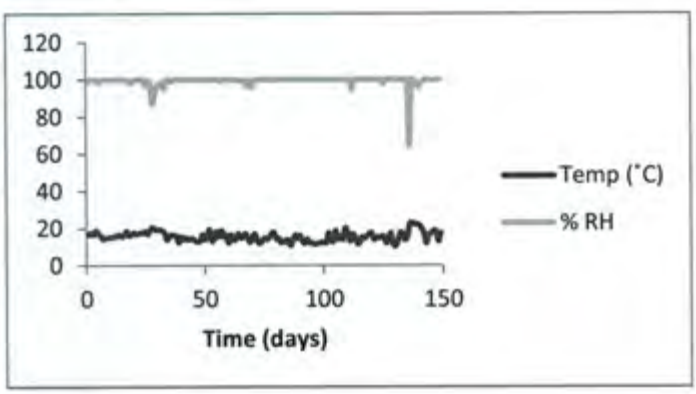
1950 m

a)

b)



c)



d)

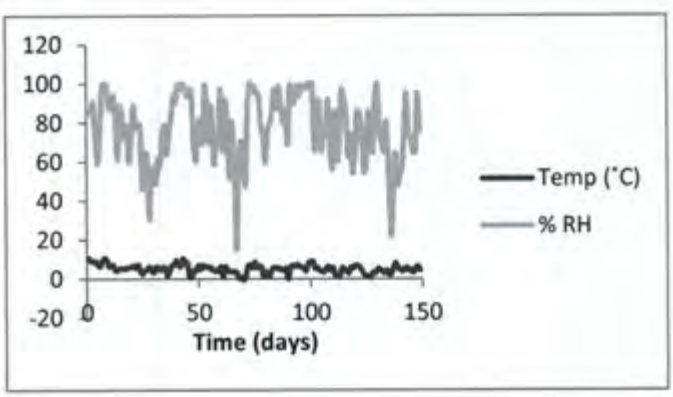
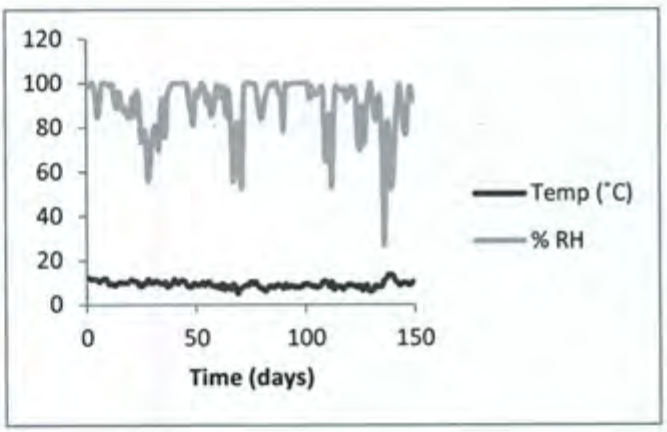


Figure 9: a) *Philipia* thickets at the 1950 m site. Temperature and relative humidity data over the 5 month period at 1950 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

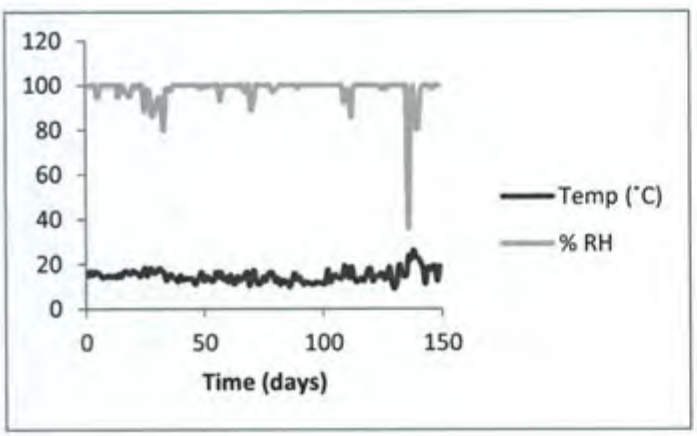
2150 m

a)

b)



c)



d)

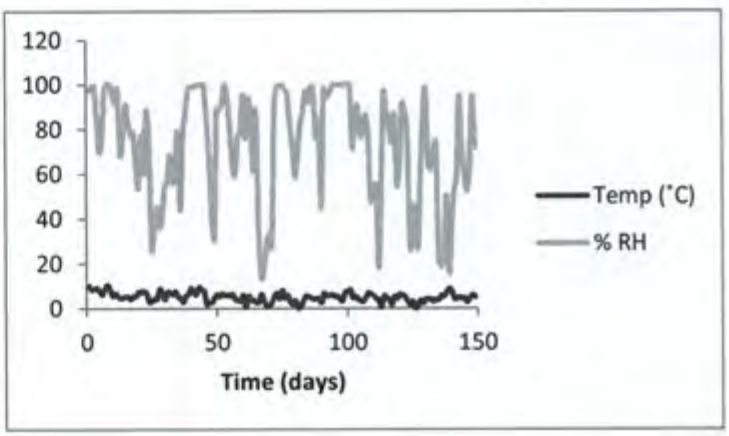
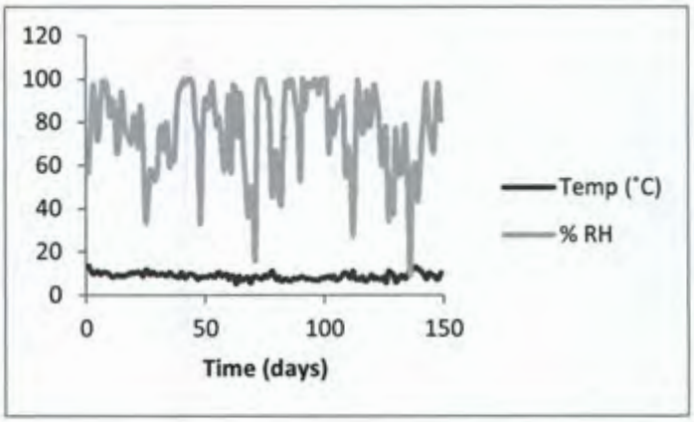


Figure 10: a) *Philipia* thickets at the 2150 m site. Temperature and relative humidity data over the 5 month period at 2150 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

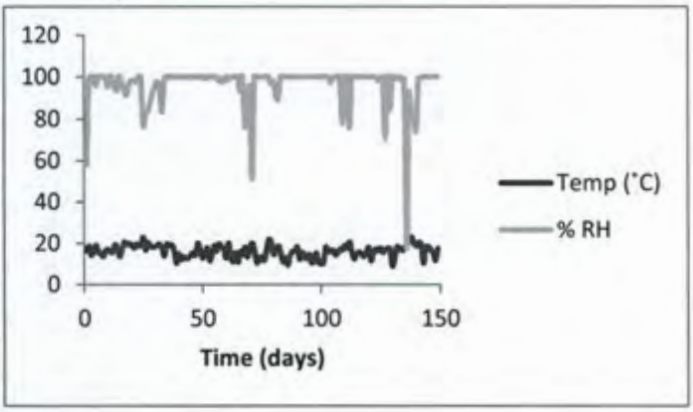
2350 m

a)

b)



c)



d)

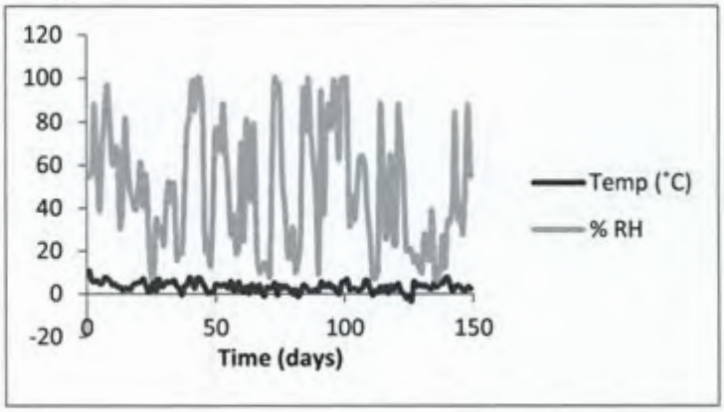
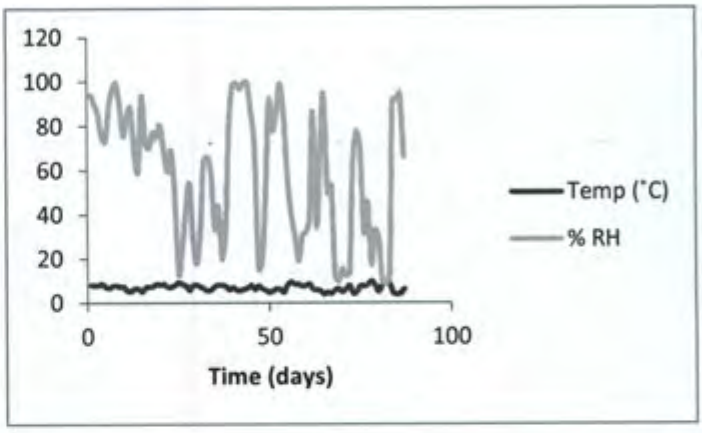


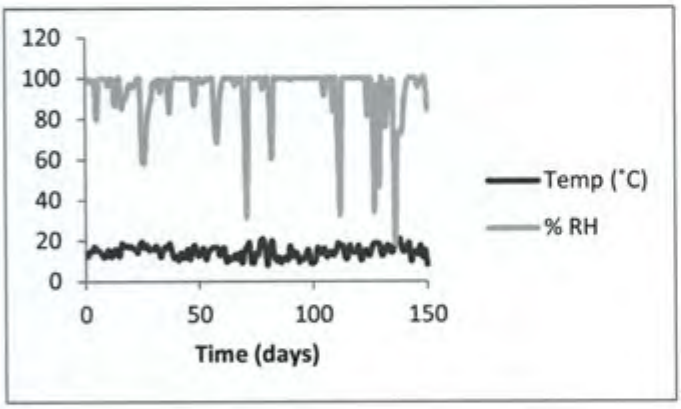
Figure 11: a) Shrubland at the 2350 m site. Temperature and relative humidity data over the 5 month period at 2350 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

2550 m

a)



b)



c)

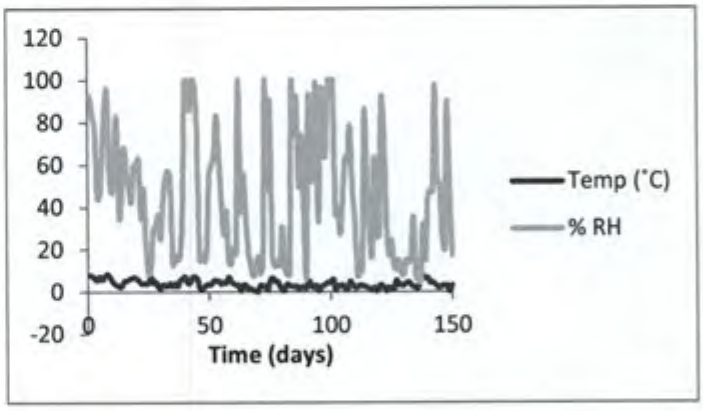
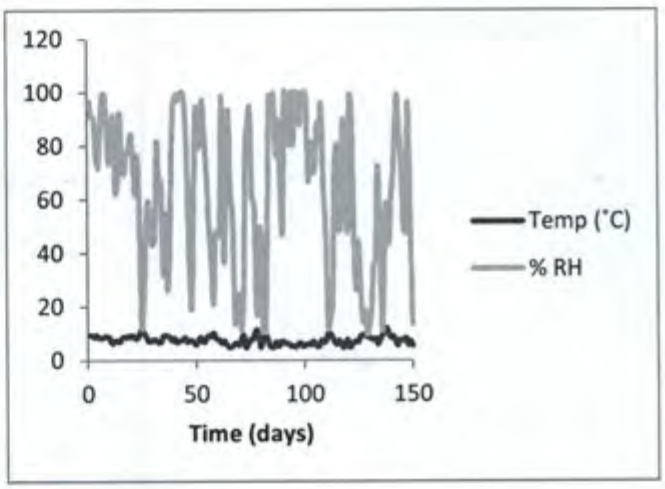


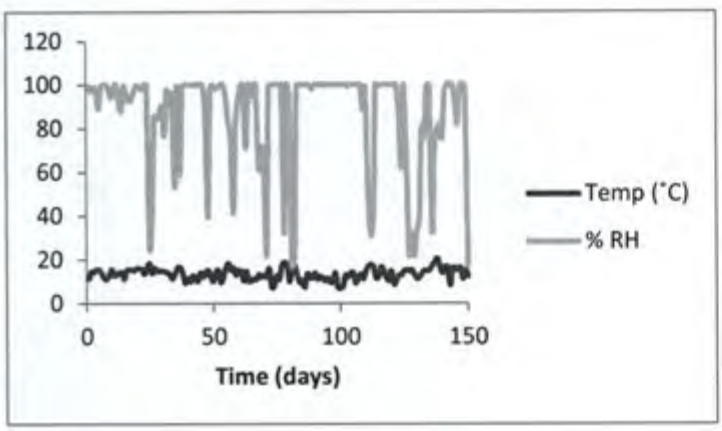
Figure 12: a) Shrubland at the 2550 m site. Temperature and relative humidity data over the 5 month period at 2550 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

2750 m

a)



b)



c)

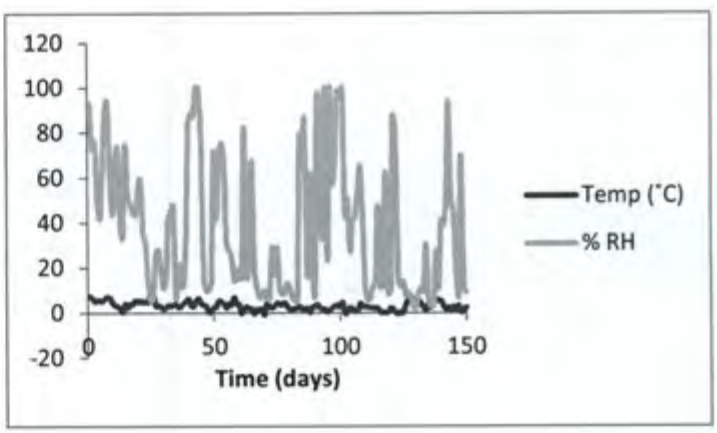


Figure 13: Alpine shrubland at the 2750 m site. Temperature and relative humidity data over the 5 month period at 2750 m. b) Daily mean temperature and humidity (mean of hourly values). c) Daily maximum temperature and humidity and d) Daily minimum temperature and humidity.

Table 1: Regression analyses of bryophyte functional traits with altitude

Functional trait	R^2	F	p
Ocelli	0.98	210.01	0.0000001
Secondary pigments	0.86	54.02	0.00004
Dissected leaves	0.85	23.55	0.0004
Trigones	0.61	13.88	0.005
Lobule presence	0.54	4.67	0.045
Underleaf length	0.80	14.21	0.003
Lobule:leaf ratio	0.75	26.46	0.001
Leaf length	0.65	7.46	0.015
Gametophyte length	0.49	8.52	0.017
Stem diameter	0.54	4.70	0.045

	Species	LL1	LD	PP	GL	GW	EI	SD	UP	UL	LP	LL2	RL	TP	OP	SP
1	***Acrolejeunea emergens* var. *emergens*** (Mitt.) Steph.	0.85	0.00	1.00	20.00	1.25	16.00	0.15	1.00	0.53	1.00	0.45	0.53	1.00	0.00	0.00
2	***Adelanthus decipiens*** (Hook.) Mitt.	1.50	1.00	0.00	35.00	2.25	15.56	0.23	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
3	***Amazoopsis diplopoda*** (Pocs) J.J.Engel et G.L.S.Merr.	0.60	1.00	1.00	5.00	0.75	6.67	0.16	1.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
4	***Anastrophyllum auritum*** (Lehm.) Steph.	0.70	1.00	0.00	30.00	1.10	27.27	0.25	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
5	***Anastrophyllum minutum*** (Schreb.) R.M.Schust.	0.60	1.00	0.00	7.50	1.10	6.82	0.15	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
6	***Anastrophyllum piligerum*** (Reinw., Blume & Nees) Steph.	1.20	1.00	0.00	11.00	1.80	6.11	0.20	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
7	***Andrewsianthus aberrans*** (Nees & Mont.) Grolle	0.48	1.00	0.00	11.50	0.80	14.38	0.19	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
8	***Andrewsianthus cf. bilobus*** (Mitt.) Grolle	0.73	1.00	0.00	14.60	1.30	11.23	0.18	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
9	***Aneura latissima Spruce*** *	na	na	0.00	55.00	45.00	1.22	na	na	na	na	na	na	0.00	0.00	0.00
10	***Bazzania decrescens*** (Lehm. & Lindenb.) Trevis.	1.50	1.00	0.00	25.00	3.00	8.33	0.36	1.00	0.53	0.00	0.00	0.00	1.00	0.00	0.00
11	***Bazzania decrescens* ssp. *molleri*** Steph.	0.95	1.00	0.00	25.00	2.00	12.50	0.18	1.00	0.53	0.00	0.00	0.00	1.00	0.00	0.00
12	***Bazzania mascarena*** (Steph.) Herzog	0.79	0.00	0.00	15.00	1.25	12.00	0.41	1.00	0.38	0.00	0.00	0.00	1.00	0.00	0.00
13	***Bazzania nitida*** (F.Weber) Grolle	1.10	0.00	0.00	15.00	1.40	10.71	0.15	1.00	0.33	0.00	0.00	0.00	1.00	0.00	0.00
14	***Bazzania praerupta*** (Reinw., Blume & Nees) Trevis.	1.85	1.00	0.00	20.00	2.95	6.78	0.35	1.00	0.97	0.00	0.00	0.00	1.00	0.00	1.00
15	***Bazzania roccatii*** Gola	1.25	1.00	0.00	2.00	2.00	na	0.22	1.00	0.35	0.00	0.00	0.00	1.00	0.00	1.00
16	***Calypogeia afrocaerulea*** E.W.Jones	1.25	1.00	0.00	18.00	2.75	6.55	0.28	1.00	0.50	0.00	0.00	0.00	0.00	0.00	1.00
17	***Calypogeia arguta*** Nees & Mont.	0.95	1.00	1.00	20.00	1.75	11.43	0.15	1.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00
18	***Calypogeia fissa*** (L.) Raddi	1.40	1.00	0.00	30.00	2.50	12.00	0.25	1.00	0.30	0.00	0.00	0.00	0.00	0.00	1.00
19	***Calypogeia mascarenensis*** Bisch.	1.50	1.00	0.00	2.60	2.55	1.02	0.29	1.00	0.54	0.00	0.00	0.00	0.00	0.00	1.00
20	***Cephalozia connivens* ssp. *fissa*** Váňa	0.37	1.00	0.00	11.50	1.05	10.95	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21	***Cephaloziella kiaeri*** (Austin) Douin	0.15	1.00	1.00	6.50	0.40	16.25	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
22	***Cephaloziella vaginans*** Steph.	0.13	1.00	1.00	10.00	0.44	22.73	0.08	1.00	0.06	0.00	0.00	0.00	0.00	0.00	1.00
23	***Ceratolejeunea belangeriana*** (Gottsche) Steph. *	0.95	0.00	0.00	32.50	1.25	26.00	na	1.00	na	1.00	0.24	0.25	1.00	1.00	1.00
24	***Ceratolejeunea calabariensis*** Steph.	0.65	0.00	0.00	20.00	1.25	16.00	0.09	1.00	0.38	1.00	0.10	0.15	1.00	1.00	1.00
25	***Ceratolejeunea cornuta*** (Lindenb.) Schiffn.,	0.64	0.00	0.00	30.00	1.30	23.08	0.07	1.00	0.09	1.00	0.09	0.14	1.00	1.00	1.00
26	***Ceratolejeunea zenkeri*** Steph.	0.66	0.00	0.00	20.00	1.25	16.00	0.09	1.00	0.40	1.00	0.15	0.23	0.00	1.00	1.00
27	***Cheilolejeunea cordistipula*** (Steph.) Grolle ex E.W.Jones	0.73	0.00	0.00	35.00	1.13	31.11	0.08	1.00	0.36	1.00	0.31	0.43	1.00	0.00	0.00
28	***Cheilolejeunea decursiva*** (Sande Lac.) R.M.Schust.	0.38	0.00	0.00	12.50	0.58	21.74	0.05	1.00	0.13	1.00	0.14	0.36	1.00	0.00	0.00
29	***Cheilolejeunea montagnei*** (Gottsche) R.M.Schust.	0.73	0.00	0.00	20.00	1.10	18.18	0.13	1.00	0.45	1.00	0.17	0.23	1.00	0.00	1.00
30	***Cheilolejeunea serpentina*** (Mitt.) Mizut.	0.43	0.00	0.00	17.50	0.90	19.44	0.07	1.00	0.30	1.00	0.12	0.28	1.00	0.00	1.00
31	***Cheilolejeunea surrepens*** (Mitt.) E.W.Jones	0.60	0.00	0.00	30.00	1.10	27.27	0.07	1.00	0.40	1.00	0.28	0.47	1.00	0.00	0.00
32	***Cheilolejeunea trifaria*** (Reinw., Blume et Nees) Mizut.	0.55	0.00	0.00	20.00	0.85	23.53	0.11	1.00	0.43	1.00	0.12	0.22	1.00	0.00	0.00
33	***Cheilolejeunea usambarana*** (Steph.) Grolle	0.40	0.00	0.00	35.00	0.70	50.00	0.10	1.00	0.23	1.00	0.16	0.40	1.00	0.00	1.00
34	***Chiloscyphus coadunatus*** (Sw.) J.J.Engel et R.M.Schust.	1.50	1.00	0.00	80.00	3.30	24.24	0.06	1.00	1.20	0.00	0.00	0.00	1.00	0.00	0.00
35	***Chiloscyphus concretus*** (Mont.) J.J.Engel et R.M.Schust.	0.90	0.00	0.00	20.00	1.80	11.11	0.17	1.00	0.24	0.00	0.00	0.00	1.00	0.00	0.00
36	***Chiloscyphus difformis*** (Nees) J.J.Engel et R.M.Schust.	1.00	1.00	0.00	20.00	1.75	11.43	0.16	1.00	0.20	0.00	0.00	0.00	1.00	0.00	1.00
37	***Chiloscyphus martianus*** (Nees) J.J.Engel et R.M.Schust.	1.35	1.00	0.00	50.00	3.00	16.67	0.19	1.00	0.32	0.00	0.00	0.00	1.00	0.00	0.00
38	***Chiloscyphus muricatus*** (Lehm.) J.J.Engel et R.M.Schust.	0.75	1.00	0.00	20.00	1.75	11.43	0.25	1.00	0.45	0.00	0.00	0.00	0.00	0.00	1.00
39	***Cololejeunea ceatocarpa*** (Ångstr.) Steph.	0.55	0.00	0.00	7.50	1.15	6.52	0.05	0.00	0.00	1.00	0.28	0.50	0.00	0.00	1.00
40	***Cololejeunea haskarliana*** (Lehm. & Lindenb.) Schiffn.	0.40	1.00	1.00	5.00	0.80	6.25	0.05	0.00	0.00	1.00	0.15	0.38	0.00	0.00	1.00
41	***Cololejeunea hildebrandii*** (Austin) Steph.	0.55	0.00	0.00	10.00	1.00	10.00	0.04	0.00	0.00	1.00	0.29	0.53	0.00	0.00	0.00
42	***Cololejeunea obliqua*** (Nees & Mont.) Schiffn.	0.75	0.00	1.00	10.00	1.30	7.69	0.05	0.00	0.00	1.00	0.28	0.37	1.00	0.00	0.00
43	***Cololejeunea peponiformis*** Mizut.	0.30	0.00	0.00	1.50	0.50	3.00	0.05	0.00	0.00	1.00	0.15	0.50	0.00	0.00	1.00
44	***Cololejeunea tanzaniae*** Pócs	0.75	0.00	0.00	12.50	1.25	10.00	0.06	0.00	0.00	1.00	0.28	0.37	1.00	0.00	0.00
45	***Cololejeunea zenkeri*** (Steph.) E.W.Jones	0.63	0.00	1.00	10.00	1.05	9.52	0.05	0.00	0.00	1.00	0.23	0.36	1.00	0.00	0.00
46	***Colura benoistii*** Ast	2.00	0.00	0.00	10.00	2.40	4.17	0.07	1.00	0.40	1.00	0.55	0.28	1.00	0.00	0.00
47	***Colura calyptrifolia*** (Hook.) Dumort.	1.15	0.00	0.00	5.00	1.50	3.33	0.06	1.00	0.13	1.00	0.30	0.26	0.00	0.00	1.00
48	***Colura digitalis*** (Mitt.) Steph.	1.45	0.00	0.00	10.00	1.10	9.09	0.13	1.00	0.32	1.00	0.45	0.31	1.00	0.00	1.00
49	***Colura humbertii*** Jov.-Ast *	1.35	0.00	0.00	4.50	0.90	5.00	na	1.00	na	1.00	0.60	0.44	0.00	0.00	0.00
50	***Colura obesa*** Ast	1.35	0.00	0.00	3.50	1.40	2.50	0.10	1.00	0.20	1.00	0.40	0.30	1.00	0.00	1.00
51	***Colura tenuicornis*** (A.Evans) Steph.	1.25	0.00	0.00	4.00	1.88	2.13	0.08	1.00	0.25	1.00	0.55	0.44	1.00	0.00	0.00
52	***Conoscyphus trapezioides*** (Sande Lac.) Schiffn.	1.20	0.00	0.00	7.50	2.25	3.33	0.14	1.00	0.65	0.00	0.00	0.00	1.00	0.00	1.00
53	***Dendroceros borbonicus*** Steph. *	na	na	na	2.25	0.90	2.50	na	na	na	na	na	na	1.00	0.00	0.00
54	***Diplasiolejeunea cavifolia*** Steph.	1.00	0.00	0.00	22.50	1.50	15.00	0.05	1.00	0.33	1.00	0.50	0.50	0.00	1.00	1.00
55	***Diplasiolejeunea cogoensis*** Infante, Heras et Pócs	1.10	0.00	0.00	10.00	2.60	3.85	0.14	1.00	0.38	1.00	0.43	0.39	0.00	1.00	1.00
56	***Diplasiolejeunea cornuta*** Steph.	0.70	0.00	0.00	15.00	0.85	17.65	0.06	1.00	0.10	1.00	0.32	0.45	1.00	0.00	1.00
57	***Drepanolejeunea cultrella*** (Mitt.) Steph.	0.28	0.00	0.00	30.00	0.38	80.00	0.04	1.00	0.07	1.00	0.11	0.41	0.00	1.00	0.00

	Species	LL1	LD	PP	GL	GW	EI	SD	UP	UL	LP	LL2	RL	TP	OP	SP
58	***Drepanolejeunea helenae*** Pócs	0.40	0.00	0.00	22.50	0.73	31.03	0.06	1.00	0.10	1.00	0.15	0.38	0.00	1.00	1.00
59	***Drepanolejeunea madagascariensis*** (Steph.) Grolle	0.80	0.00	0.00	10.00	1.25	8.00	0.07	1.00	0.10	1.00	0.27	0.34	0.00	1.00	0.00
60	***Drepanolejeunea physaefolia*** (Gottsche) Steph.	0.35	0.00	1.00	5.50	0.48	11.58	0.05	1.00	0.05	1.00	0.18	0.50	1.00	1.00	1.00
61	***Drepanolejeunea trematodes*** (Nees) Bischl.	0.64	0.00	0.00	10.00	0.88	11.43	0.05	1.00	0.12	1.00	0.27	0.41	1.00	1.00	0.00
62	***Frullania angulata*** Mitt. var. ***angulata***	1.40	0.00	0.00	125.00	1.55	80.65	0.15	1.00	0.90	1.00	0.27	0.19	1.00	0.00	1.00
63	***Frullania apicalis*** Mitt.	0.65	1.00	0.00	37.50	0.98	38.46	0.14	1.00	0.28	1.00	0.24	0.36	1.00	0.00	1.00
64	***Frullania apiculata*** (Reinw., Blume & Nees) Nees	0.70	1.00	0.00	50.00	1.05	47.62	0.15	1.00	0.37	1.00	0.21	0.29	1.00	0.00	1.00
65	***Frullania borbonica*** Lindenb.	0.53	0.00	0.00	15.00	1.00	15.00	0.10	1.00	0.19	1.00	0.18	0.34	1.00	0.00	0.00
66	***Frullania capensis*** Gottsche	0.60	0.00	0.00	20.00	1.05	19.05	0.11	1.00	0.13	1.00	0.06	0.10	1.00	0.00	1.00
67	***Frullania grossiclava*** Steph.	1.20	0.00	0.00	30.00	1.55	19.35	0.20	1.00	0.53	1.00	0.45	0.38	1.00	0.00	1.00
68	***Frullania humbertii*** Vanden Berghen	0.70	0.00	0.00	27.50	1.25	22.00	0.14	1.00	0.47	1.00	0.20	0.29	1.00	0.00	1.00
69	***Frullania lindenbergii*** Lehm.	1.10	0.00	0.00	25.00	2.00	12.50	0.19	1.00	0.50	1.00	0.36	0.33	1.00	0.00	1.00
70	***Frullania repandistipula*** Sande Lac.	0.95	0.00	0.00	25.00	1.23	20.41	0.12	1.00	0.40	1.00	0.21	0.22	1.00	0.00	1.00
71	***Frullania schimperi*** var. ***schimperi*** Nees	0.95	0.00	0.00	5.00	1.20	4.17	0.25	1.00	0.73	1.00	0.28	0.29	1.00	0.00	1.00
72	***Frullania serrata*** Gottsche	1.05	1.00	0.00	85.00	1.38	61.82	0.24	1.00	0.75	1.00	0.27	0.26	1.00	0.00	1.00
73	***Frullania usambarana*** var. ***reducta*** Vanden Berghen	1.10	0.00	0.00	30.00	1.80	16.67	0.16	1.00	0.47	1.00	0.53	0.48	1.00	0.00	1.00
74	***Frullania variegata*** Steph.	0.80	0.00	0.00	22.50	1.15	19.57	0.14	1.00	0.31	1.00	0.41	0.51	1.00	0.00	1.00
75	***Gottschea sphagnoides*** (Schwägr.) Lindb.	3.50	1.00	0.00	15.00	7.50	2.00	0.36	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
76	***Gottschelia schizopleura*** (Spruce) Grolle	1.90	0.00	0.00	25.00	2.75	9.09	0.27	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
77	***Haplolejeunea cucullata*** (Steph.) Grolle	0.40	0.00	0.00	6.20	0.65	9.54	0.05	1.00	0.18	1.00	0.12	0.30	1.00	1.00	0.00
78	***Herbertus dicranus*** (Taylor ex Gottsche, Lindenb. & Nees) Trevis.	2.68	1.00	1.00	23.00	2.48	25.58	0.24	1.00	0.20	0.00	0.00	0.00	1.00	0.00	1.00
79	***Herbertus mauritianus*** N.G. Hodgetts	2.50	1.00	1.00	100.00	0.90	111.11	0.33	1.00	1.35	0.00	0.00	0.00	1.00	0.00	1.00
80	***Heteroscyphus dubius*** (Gottsche) Schiffn.	1.50	0.00	0.00	55.00	2.25	24.44	0.20	1.00	0.40	0.00	0.00	0.00	1.00	0.00	0.00
81	***Heteroscyphus*** sp nov.	1.80	0.00	0.00	15.00	2.00	7.50	0.23	1.00	0.80	0.00	0.00	0.00	1.00	0.00	0.00
82	***Heteroscyphus splendens*** (Lehm. et Lindenb.) Grolle *	2.85	0.00	0.00	50.00	4.25	11.76	na	1.00	na	0.00	0.00	0.00	1.00	0.00	1.00
83	***Isotachis auhertii*** (Schwägr.) Mitt.	1.25	1.00	0.00	30.00	na	na	0.30	1.00	0.58	0.00	0.00	0.00	1.00	0.00	1.00
84	***Jamesoniella contracta*** (Reinw., Blume & Nees) N.Kitag.	1.38	0.00	1.00	22.50	2.00	11.25	0.25	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
85	***Jamesoniella purpurascens*** Steph.	1.45	0.00	0.00	55.00	2.13	25.88	0.19	1.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
86	***Jungermannia borgenii*** Gottsche ex Pearson	1.20	0.00	0.00	18.50	1.75	10.57	0.31	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
87	***Jungermannia onraedtii*** Váňa	0.60	0.00	0.00	10.00	0.70	14.29	0.25	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
88	***Kurzia capillaris*** ssp. ***stephanii*** (Renauld ex Steph.) Pócs	0.18	1.00	1.00	40.00	0.52	76.92	0.09	1.00	0.09	0.00	0.00	0.00	0.00	0.00	1.00
89	***Kurzia capillaris subsp. capillaris*** (Sw.) Grolle	0.16	1.00	1.00	30.00	0.35	85.71	0.07	1.00	0.09	0.00	0.00	0.00	0.00	0.00	1.00
90	***Lejeunea alata*** Gottsche	0.60	0.00	0.00	10.00	1.10	9.09	0.12	1.00	0.20	1.00	0.20	0.33	1.00	0.00	0.00
91	***Lejeunea rodriguezii*** (Steph.)	0.23	0.00	0.00	2.80	0.47	6.02	0.04	1.00	0.07	1.00	0.06	0.24	1.00	0.00	0.00
92	***Lejeunea cantabrigiensis*** E.W.Jones *	0.40	0.00	1.00	na	0.70	na	0.07	1.00	0.25	1.00	0.21	0.53	1.00	0.00	0.00
93	***Lejeunea confusa*** E.W. Jones	0.23	0.00	0.00	15.00	0.55	27.27	0.07	1.00	0.10	1.00	0.09	0.42	1.00	0.00	0.00
94	***Lejeunea eckloniana*** Lindenb.	0.62	0.00	0.00	10.00	1.10	9.09	0.10	1.00	0.32	1.00	0.14	0.22	1.00	0.00	1.00
95	***Lejeunea flava*** (Sw.) Nees subsp. ***flava*** Schuster	0.63	0.00	0.00	25.00	1.15	21.74	0.16	1.00	0.40	1.00	0.21	0.34	1.00	0.00	0.00
96	***Lejeunea lamana*** E.W.Jones	0.50	0.00	0.00	7.00	1.00	7.00	0.09	1.00	0.20	1.00	0.22	0.44	0.00	0.00	0.00
97	***Lejeunea obtusata*** Gottsche	0.50	0.00	0.00	10.00	0.60	16.67	0.09	1.00	0.20	1.00	0.13	0.26	1.00	0.00	0.00
98	***Lejeunea ramosissima*** Steph.	0.68	0.00	0.00	25.00	1.15	21.74	0.10	1.00	0.55	1.00	0.14	0.20	1.00	0.00	0.00
99	***Lejeunea tabularis*** (Sprengl.) Gottsche *et al.*	0.60	0.00	0.00	25.00	1.20	20.83	0.10	1.00	0.30	1.00	0.14	0.23	1.00	0.00	1.00
100	***Lejeunea tuberculosa*** Steph.	0.35	0.00	0.00	15.00	0.65	23.08	0.05	1.00	0.21	1.00	0.13	0.37	1.00	0.00	0.00
101	***Lejeunea villaumei*** (Steph.) Grolle	0.62	0.00	0.00	10.00	0.95	10.53	0.08	1.00	0.30	1.00	0.18	0.29	1.00	0.00	0.00
102	***Lepidolejeunea delessertii*** (Nees et Mont.) Grolle	0.35	1.00	0.00	15.00	0.90	16.67	0.05	1.00	0.24	1.00	0.09	0.26	1.00	1.00	1.00
103	***Lepidozia africana*** Steph. *	0.19	1.00	0.00	45.00	0.35	128.57	0.16	1.00	0.19	0.00	0.00	0.00	0.00	0.00	1.00
104	***Lepidozia stuhlmannii Steph.***	0.40	1.00	0.00	20.00	0.90	22.22	0.21	1.00	0.22	0.00	0.00	0.00	1.00	0.00	1.00
105	***Lepidozia stuhlmannii*** subsp. ***pulvinata*** (Steph.) Pócs	0.35	1.00	0.00	20.00	0.30	66.67	0.21	1.00	0.13	0.00	0.00	0.00	1.00	0.00	1.00
106	***Leptolejeunea maculata*** (Mitt.) Schiffn.	0.65	1.00	0.00	25.00	0.90	27.78	0.06	1.00	0.13	1.00	0.27	0.42	1.00	1.00	0.00
107	***Leptoscyphus infuscatus*** (Mitt.) E.W.Jones	1.55	1.00	0.00	15.00	2.75	5.45	0.18	1.00	0.59	0.00	0.00	0.00	1.00	0.00	1.00
108	***Leucolejeunea xanthocarpa*** (Lehm. & Lindenb.) A.Evans	0.85	0.00	0.00	20.00	1.40	14.29	0.13	1.00	0.50	1.00	0.43	0.50	1.00	0.00	0.00
109	***Lophocolea bidentata*** (L.) Dumort.	1.50	1.00	0.00	10.00	3.00	3.33	0.19	1.00	0.41	0.00	0.00	0.00	0.00	0.00	1.00
110	***Lopholejeunea borbonica*** Steph.	0.80	0.00	0.00	35.00	1.40	25.00	0.13	1.00	0.38	1.00	0.29	0.36	1.00	0.00	1.00
111	***Lopholejeunea eulopha*** (Taylor) Schiffn.	1.15	0.00	0.00	35.00	2.00	17.50	0.18	1.00	0.61	1.00	0.29	0.25	1.00	0.00	1.00
112	***Lopholejeunea multilacera*** Steph.	0.85	0.00	0.00	20.00	1.10	18.18	0.18	1.00	0.56	1.00	0.20	0.24	0.00	0.00	1.00
113	***Lopholejeunea nigricans*** (Lindenb.) Schiffn.	0.68	0.00	0.00	20.00	1.25	16.00	0.13	1.00	0.31	1.00	0.23	0.33	1.00	0.00	0.00
114	***Lopholejeunea subfusca*** (Nees) Schiffn.	0.74	0.00	0.00	15.00	1.30	11.54	0.12	1.00	0.40	1.00	0.23	0.31	1.00	0.00	1.00

	Species	LLI	LD	PP	GL	GW	EI	SD	UP	UL	LP	LL2	RL	TP	OP	SP
115	*Marchesinia madagassa* Steph.	1.05	0.00	0.00	40.00	1.65	24.24	0.20	1.00	0.65	1.00	0.35	0.33	1.00	0.00	1.00
116	*Mastigophora diclados* (Brid. ex F.Weber) Nees	0.80	1.00	0.00	110.00	0.85	129.41	0.30	1.00	0.50	0.00	0.00	0.00	1.00	0.00	1.00
117	*Metzgeria consanguinea* Schiffn. *	na	na	0.00	25.00	0.90	27.78	na	na	na	na	na	na	0.00	0.00	1.00
118	*Metzgeria furcata* (L.) Dumort. *	na	na	0.00	15.00	0.80	18.75	na	na	na	na	na	na	0.00	0.00	1.00
119	*Metzgeria leptoneura* Spruce *	na	na	0.00	35.00	1.60	21.88	na	na	na	na	na	na	0.00	0.00	1.00
120	*Microlejeunea africana* Steph.	0.21	0.00	0.00	1.50	0.23	6.52	0.04	1.00	0.11	1.00	0.10	0.50	1.00	1.00	0.00
121	*Microlejeunea ankasica* E.W.Jones (new)	0.21	0.00	0.00	2.10	0.40	5.25	0.03	1.00	0.09	1.00	0.13	0.63	0.00	0.00	0.00
122	*Microlejeunea dispar* Ast	0.35	0.00	0.00	4.00	0.40	10.00	0.04	1.00	0.11	1.00	0.25	0.71	1.00	0.00	0.00
123	*Microlejeunea inflata* Steph.	0.41	0.00	0.00	3.00	0.60	5.00	0.05	1.00	0.10	1.00	0.20	0.49	0.00	0.00	0.00
124	*Microlejeunea kamerunensis* Steph.	0.32	0.00	0.00	3.00	0.48	6.32	0.06	1.00	0.08	1.00	0.10	0.32	1.00	1.00	0.00
125	*Microlejeunea oblongistipula* (Gottsche) Pearson	0.41	0.00	0.00	30.00	0.60	50.00	0.05	1.00	0.07	1.00	0.14	0.33	1.00	1.00	0.00
126	*Microlejeunea strasbergii* Bardat & Ah-Peng	0.13	0.00	0.00	1.75	0.18	10.00	0.06	1.00	0.07	1.00	0.10	0.80	1.00	0.00	1.00
127	*Mnioloma fuscum* (Lehm.) R. M. Schust.	0.75	0.00	0.00	7.00	1.65	4.24	0.15	1.00	0.30	0.00	0.00	0.00	1.00	0.00	1.00
128	*Plagiochila angusta* Lindenb.	1.45	1.00	0.00	45.00	2.65	16.98	0.30	1.00	0.06	0.00	0.00	0.00	1.00	0.00	1.00
129	*Plagiochila drepanophylla* Sande Lac.	2.10	1.00	0.00	35.00	4.05	8.64	0.30	1.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
130	*Plagiochila pectinata* Willd. ex Lindenb.	2.00	1.00	0.00	75.00	4.90	15.31	0.38	1.00	0.14	0.00	0.00	0.00	1.00	0.00	1.00
131	*Plagiochila renauldii* Steph.	1.55	0.00	0.00	55.00	3.00	18.33	0.38	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
132	*Plagiochila repanda* (Schwägr.) Lindenb.	2.00	0.00	0.00	125.00	4.00	31.25	0.35	1.00	0.10	0.00	0.00	0.00	1.00	0.00	0.00
133	*Plagiochila rodriguezii* Steph.	1.70	0.00	0.00	55.00	3.50	15.71	0.35	1.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00
134	*Plagiochila terebrans* Nees & Mont. ex Lindenb.	2.20	1.00	0.00	65.00	4.25	15.29	0.40	1.00	0.15	0.00	0.00	0.00	1.00	0.00	1.00
135	*Pleurozia gigantea* (F. Weber) Lindb.	3.50	1.00	0.00	75.00	3.75	20.00	0.69	0.00	0.00	1.00	1.90	0.54	1.00	0.00	1.00
136	*Plicanthus hirtellus* (F.Weber) Mitt.	1.55	1.00	0.00	100.00	2.00	50.00	0.35	1.00	0.80	0.00	0.00	0.00	1.00	0.00	1.00
137	*Prionolejeunea grata* (Gottsche) Schiffn.	0.33	0.00	0.00	0.70	0.10	7.00	0.07	1.00	0.17	1.00	0.11	0.33	0.00	0.00	0.00
138	*Radula ankefinensis* Gottsche ex Steph.	1.05	0.00	0.00	20.00	3.25	6.15	0.17	0.00	0.00	1.00	0.42	0.40	0.00	0.00	0.00
139	*Radula appressa* Mitt.	1.15	0.00	1.00	35.00	1.80	19.44	0.18	0.00	0.00	1.00	0.26	0.23	0.00	0.00	1.00
140	*Radula boryana* (F. Weber) Mont.	1.75	0.00	0.00	100.00	2.75	36.36	0.30	0.00	0.00	1.00	0.35	0.20	1.00	0.00	1.00
141	*Radula comorensis* Steph.	0.90	0.00	0.00	25.00	1.65	15.15	0.23	0.00	0.00	1.00	0.35	0.39	1.00	0.00	1.00
142	*Radula evelynae* Yamada	0.98	0.00	0.00	15.00	1.60	9.38	0.13	0.00	0.00	1.00	0.45	0.46	1.00	0.00	1.00
143	*Radula fulvifolia* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees *	0.75	0.00	0.00	27.50	na	na	0.16	0.00	0.00	1.00	0.30	0.40	0.00	0.00	1.00
144	*Radula madagascariensis* Gottsche	0.75	0.00	0.00	15.00	1.50	10.00	0.11	0.00	0.00	1.00	0.38	0.50	1.00	0.00	1.00
145	*Radula stenocalyx* Mont.	0.90	0.00	0.00	10.00	1.45	6.90	0.07	0.00	0.00	1.00	0.28	0.31	1.00	0.00	0.00
146	*Radula tabularis* Steph.	1.45	0.00	0.00	20.00	1.45	13.79	0.12	0.00	0.00	1.00	0.48	0.33	1.00	0.00	1.00
147	*Radula volata* Taylor ex Gottsche, Lindenb. & Nees	1.30	0.00	0.00	40.00	0.65	61.54	0.25	0.00	0.00	1.00	0.55	0.42	1.00	0.00	1.00
148	*Riccardia amazonica* (Spruce) Schiffn. ex Gradst. *	na	na	0.00	3.00	0.40	7.50	na	na	na	na	na	na	0.00	0.00	1.00
149	*Riccardia erosa* (Steph.) E.W. Jones *	na	na	0.00	3.00	0.23	13.33	na	na	na	na	na	na	0.00	0.00	1.00
150	*Riccardia fastigiata* (Lehm.) Trev. *	na	na	0.00	17.50	0.65	26.92	na	na	na	na	na	na	0.00	0.00	0.00
151	*Riccardia limbata* (Steph.) E.W.Jones *	na	na	0.00	15.00	0.70	21.43	na	na	na	na	na	na	0.00	0.00	1.00
152	*Riccardia longispica* (Steph.) Pearson *	na	na	0.00	20.00	0.90	22.22	na	na	na	na	na	na	0.00	0.00	1.00
153	*Taxilejeunea conformis* (Mont. et Nees) Steph.	0.53	0.00	0.00	30.00	1.15	26.09	0.98	1.00	0.31	1.00	0.24	0.45	1.00	0.00	0.00
154	*Telaranea coactilis* (Spruce) Engel & Merr.	0.80	1.00	1.00	4.00	0.65	6.15	0.08	1.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00
155	*Telaranea diacantha* (Mont.) Engel et Merr.	0.60	1.00	1.00	4.00	0.65	6.15	0.07	1.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
156	*Telaranea nematodes* (Gottsche ex Austin) M.Howe	0.45	1.00	0.00	20.00	1.00	20.00	0.12	1.00	0.07	0.00	0.00	0.00	0.00	0.00	1.00

LL1	Leaf length
LD	Leaf dissection
PP	Papillae
GL	Gametophyte length
GW	Gametophyte width
EI	Elongation index
SD	Stem diameter
UP	Underleaf presence
UL	Underleaf length
LP	Lobule presence
LL2	Lobule length
RL	Lobule : leaf ratio
TP	Trigone presence
OP	Ocelli presence
SP	Secondary pigments
*	Species removed from multivariate analyses