



**Altitudinal patterns of species distribution: are these related to variation in reproductive life history traits?**



Piton des Neiges volcano, September 2008

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2009

**Honours Project**

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## **Abstract**

**Aims.** To document patterns in elevational diversity of corticolous bryophytes on a tropical oceanic island. Try to relate diversity patterns to species biology, with particular emphasis on reproductive life history traits.

**Location.** The study was conducted on La Réunion island (Mascarene archipelago), on the Piton des Neiges volcano (350 - 2750 m above sea level).

**Methods.** We surveyed corticolous bryophyte assemblages of 50 cm<sup>2</sup> in three quadrats of 2 X 2 m, randomly chosen in two 10 X 10 plots every 200 m, from 350 m to 2750 m above sea level. Life history traits (sexuality, spore size and spore number) were recorded for the main species occurring along the gradient.

**Results.** A hump-shaped pattern of diversity was documented, with the highest diversity at 1350 m. Overall diversity is dominated by liverworts, except at the upper elevations. Rare species with narrow altitudinal ranges are found at the limits of the gradient. Monoicy is the prevalent sexual condition in mosses, especially at the gradient limits, while dioicy is prevalent in liverworts. Spore size and number varied strongly with altitude. Spore size was found to be lowest at mid-elevations, increasing in upper and lower elevations. Spore number was highest at mid-elevations and decreased in number in upper and lower elevations.

**Main conclusions.** Richness is closely linked with ideal climate conditions and distribution of vascular plants. Variation in reproductive life history strategies is likely to play an important role governing the distribution and abundance of species.

**Keywords:** altitudinal gradient, bryophytes, La Réunion, Life history, corticolous microhabitat

## Acknowledgements

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## INTRODUCTION

The question of how organisms adapt to complex environments (both genetically and plastically) lies at the very heart of ecology and evolutionary biology, and is of special concern in the face of rapidly changing climatic conditions at the global scale (Murray, 2002).

One of the major environmental gradients on earth after latitude is the altitudinal gradient. Many studies have documented patterns of diversity along elevational gradients (Rahbek, 1995; Kessler, 2001; Lomolino, 2001; McCain, 2004; Rahbek, 2005). The altitudinal gradient was long believed to mirror the latitudinal gradient in richness because both span a transition from warm to cold climatic conditions (Rahbek, 1995). Accordingly, species richness was considered to decline monotonically towards high elevations. Rahbek (1995, 2005) showed that this perception was the result of an overemphasis on a few studies showing such monotonic declines, but that across nearly all taxonomic groups the majority of studies (see (Vetaas & Grytnes, 2002; Bhattarai & Vetaas, 2003; Bhattarai *et al.*, 2004; Rahbek, 2005; Grau *et al.*, 2007)) show hump-shaped richness patterns with maximum richness at some intermediate point on the gradient (Kessler, 2009).

In comparison to the large literature on patterns of species distribution along elevational gradients, the distribution of life history traits along these gradients has received little attention. This is surprising in light of the strong selective forces that appear to be acting over such short geographical distances (Sorensen *et al.*, 2004). Altitude has long been considered an important environmental factor in the evolution of life history traits (e.g., (Cody, 1966; Grant & Dunham, 1990; Mathies & R.M., 1995; Badyaev, 1997). The traits upon which natural selection acts are largely responsible for determining an organisms fitness. Thus, life-history traits comprise the fundamental units subject to the evolutionary process. Many studies have tried to identify ecologically coherent groups of species with similar life history traits (Stearns, 1976; During, 1979; Longton, 1988), subsequently paying little attention to

how specific traits might be adapted to their environment. A common prediction of models explaining life history variation among species is that traits should co-evolve in response to spatial and temporal changes in the environment to yield adaptive life history tactics or strategies (Hedderson & Longton, 1995). Life history traits are very likely to exert a profound influence on distribution, and information on variation in life history will improve understanding of distribution and maintenance of populations along climatic and habitat gradients.

Moreover in this context a thorough understanding of how life history and ecological traits vary among species in relation to their altitudinal range and rarity is central to providing a scientific basis for understanding their distribution in the long term. It is usually accepted that rare species have narrower fundamental niches than common species (Rosenweig & Lomolino, 1997), but the underlying factors explaining the limits of species distribution are still unknown.

Bryophytes are a major group of land plants, comprising three early lineages. All are characterised by a life cycle in which the haploid stage is dominant, and the vast majority reproduce both sexually and asexually. In many systems, bryophytes are a conspicuous part of the plant diversity. On La Réunion the number of bryophyte species (768 species) is equivalent to that of native angiosperms species (~ 700 species). Despite their significance, only a few studies have examined life history strategies of bryophytes (Hedderson, 1992a; Longton, 1992a; Laaka-Lindberg *et al.*, 2000a; Hassel *et al.*, 2005) and even fewer have tried to relate these strategies and traits to the distribution of species along altitudinal gradients (Frey *et al.*, 1995).

The size and number of spores produced by bryophyte species varies enormously (from 2 - 20 large spores in species of *Archidium* to ~ 80 million tiny spores in *Dawsonia*) and is believed to form an integral part of the life strategy (During 1979). Spore size and number trade-offs have often been invoked as an important part of reproductive tactics in bryophytes (During, 1979) and, since reproductive characters are arguably the most important life history traits under selection they may provide a good explanation of the distribution and success of species in the environment. This idea is supported by recent work on epiphytic bryophytes, which suggests that rates

and types of dispersal (spores and asexual propagules) may better explain structuring of metacommunities than competition-colonization trade-offs (Zartman & Nascimento, 2006; Löbel *et al.*, 2008).

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. The Indian ocean islands and East Africa are included among the global biodiversity hot spots (Myers *et al.*, 2000). This project proposes to contribute to an understanding of the ecological and historical mechanisms underlying this high species richness by studying an important but poorly known plant group in this geographical area: bryophytes

The objectives of this study are to (i) compare patterns of species richness in corticolous (living on tree bark) mosses and liverworts along an altitudinal gradient, (ii) use these data to assess whether there are life history traits that are characteristic of species with different distributional ranges, and (iii) to speculate on the advantages conferred by particular values of several life history traits (i.e. sexuality, spore size and spore number) in the environment.

## Methods and Materials

### **Study area**

Situated in the Western Indian Ocean, La Réunion (55°39'E, 21°00S), along with Rodrigues and Mauritius, is part of the Mascarene archipelago. La Réunion is the largest island in the archipelago, with an area of approximately 2512 km<sup>2</sup>. It is of recent volcanic origin (2-3 million years), created by the presently dormant Piton des Neiges volcano which is currently the longest bioclimatic gradient in the Western Indian Ocean islands extending from 0 to 3069 m a.s.l. Located on the eastern side is the Piton de La Fournaise volcano, currently one of the most active Hawaiian type volcanos in the world.

The climate on the island is predominantly tropical, with summer rainfall from November to April and a cooler, drier season from June to September. The mean annual rainfall is higher on the windward eastern coast reaching ~ 10 m annually, while the West coast receives a more conservative 525 mm of precipitation annually. Mean annual temperatures vary from 24°C along the coastline to 12 °C at around 2000 m (Météo France).

The bryological flora is very diverse, and to date 768 species (455 mosses, 308 liverworts and 5 hornworts) have been recorded, with 10,81 % endemism (Ah-Peng *et al.*, submitted). La Réunion is the most speciose island for bryophytes within the Mascarene archipelago, and compared to its sister islands, a staggering 30 % of the island is unspoiled and under the protection of the National Park since 2007.

### **Study sites**

The study was conducted at altitudinal intervals of 200 m on 15 sites ranging from 350 m to 3070 m a.s.l. on the Eastern slope of the Piton des Neiges volcano (Figure 1). The location of the study plots at the different elevations was determined by the presence of intact forest, moderate slope and accessibility. Collecting permits were obtained from the National Park for studying the various plant groups (vascular and non vascular plants). The study sites and localities are described in the appendix.

### **Sampling**

The field work was carried out during three weeks in March 2008. At each elevation, 2 plots of 10 X 10 m were set, three quadrats of 2 X 2 m were randomly chosen, and within each quadrat, three trees, when they were present, were sampled at 3 different heights, (TA: 0-50 cm, TB: 50 cm - 1m and TC = 1 -2 m); at each elevation on the tree (TA, TB, TC), 3 bryophyte samples of 10 X 5 cm (50 cm<sup>2</sup>) were collected.

This size of sampling has been shown to be representative of the diversity in a 10 X 10 m plot, as well as being the most workable size for identification and from the perspective of time allocation (Ah-Peng, 2007).

### **Species identification**

Presence - absence was recorded for all species. This provides an estimate of gamma diversity, defined as the total richness of an entire elevational zone (*sensu* Lomolino, 2001). Material was air-dried and stored in paper bags, and will later be deposited in the herbarium of La Réunion (REU). The specimen identifications were undertaken by C. Ah-Peng and N. Wilding (950 -1550 m samples), J. Bardat (1350-1750 m samples), M. Chuah-Petiot (350 -750 m samples) and T.A.J. Hedderson (1950-2350 m samples). Bryophyte nomenclature follows that of O'Shea (2006) for mosses, that of Wigginton (2009) for liverworts and hornworts, and a list of recorded species (Ah-Peng & Bardat, 2005). Species that have been identified with a *cf.* need further investigation (e.g. in some cases a fertile specimen is needed to complete the identification).

### **Collection of life history data**

Life history traits, including spores size, sexuality (i.e. dioicous or monoicous), and capsule dimensions were collected for moss species that occurred at least four times along the gradient. Many of the bryophyte species sampled, especially liverworts, have ranges that are restricted to East Africa and the adjacent Indian Ocean islands and are subsequently poorly known due to a lack of collections and local bryologists. As a result, collection of life history data for liverworts was extremely challenging.

Further, the ephemeral nature of liverwort sporophytes restricted the gathering of life history data to sexuality alone.

The life history data analysed here were collected from a wide range of literature sources by N. Wilding and J. Bardat. These sources include old bibliographical collections stored at the bryological library of the National Museum of Natural History in Paris (June 2009), the PhD work of Ah-Peng (2007) and direct examination of herbarium specimens.

The volume of capsules was assumed to resemble a cylinder with radius and length equal to those measurements obtained from the literature or herbarium specimens for capsule length and breadth. Spore volume was calculated as a sphere with a diameter equal to the average spore width for the species. The capsule volume was divided by spore size to give spore number. Estimates of spore production per capsule were based on two assumptions. First, since spore volume is small in relation to capsule volume, spores were considered to form an infinite array so that 'container margin' effects were ignored. The second assumption relates to the portion of capsule volume occupied by interspore space. This ranges from 26% if spores are tightly packed to 48% if loosely packed (Marshall & Holmes, 1988). Medium packing was assumed and 37% of capsule volume was subtracted before dividing by spore size (Hedderson & Longton, 1995).

### ***Distribution measurements***

The total size of a species range was determined by the number of altitudes encompassed by its upper and lower range. The mean altitudinal range of species was estimated by taking the mid-point between the highest and lowest altitude at which they were recorded. When determining species range it was assumed that species were present throughout the range imposed by their upper and lower limits (interpolation).

Species richness was calculated as the total number of species recorded per altitude.

To provide a simple estimate of rarity and commonness, the frequency of the species over the entire gradient (i.e. the proportion of samples in which the species occurred) was used.

### **Data analysis**

To describe the species richness patterns in relation to altitude, a generalized linear model (GLM; (McCullagh & Nelder, 1989)) was used assuming a poisson distribution of errors (Mittelbach *et al.*, 2007). The effects of overdispersion were not considered, as the primary purpose of fitted lines was to highlight general trends in the data. If the variances of the data are overdispersed, a quasi-Poisson distribution can be used to take this into account (Grau *et al.*, 2007). Richness patterns for mosses, liverworts and total bryophyte species(mosses + liverworts) were regressed against altitude and plotted for comparison. The effect of microhabitat on species richness was determined by ANOVA.

Using presence-absence of species, bryophyte assemblages were compared between each altitudinal level (beta diversity). The Jaccard index was calculated to assess similarity in species composition (Magurran, 1988). It is computed as  $1 - [2B/(1+B)]$ , where B is Bray Curtis dissimilarity. The binomial index is derived from binomial deviance under the null hypothesis that the two compared communities are equal. The index does not have a fixed upper limit, but can vary among sites with no shared species. For further discussion, see (Anderson & Millar, 2004).

Patterns of rarity and commonness in relation to altitude were determined by examining scatterplots of altitudinal range and mean altitudinal range in relation to measures of rarity and commonness. Additionally, a plot of species (including abbreviated names), ordered by ascending mean altitudinal range was included to aid visualization of trends.

Spore size and number were weighted by the total of number of samples in which the species was recorded at a given altitude. This is thought to give a closer estimate of average spore size per-sample per-altitude. A generalized additive model (GAM) with a cubic smooth spline (Hastie & Tibshirani, 1990) was used to describe patterns in spore size and spore number in relation to altitude. The GAM approach is especially useful for data exploration as it makes no *a priori* assumptions about the type of relationship being modelled. The GAM approach contrasts with the generalized linear

model approach where *a priori* assumptions about the relationships being modelled (e.g. a symmetrical humped relationship) are required.

All analysis were carried out with the statistical software R (R Development Core Team, 2009), with the packages `ade4` (Dray & Dufour, 2007) and `vegan`.

## Results

The corticolous substrate was most abundant between 550 m and 2150 m, corresponding to the distribution of the main forest patches along the gradient. Plots at 350 m and those above 2150 m had a limited number of trees, hence sampling was limited to between two and six trees at some sites.

An excess of 3132 identifications were made in the 510 samples, giving a total of 242 bryophytes species, belonging to 89 genera and 39 families, including two new species for science and many new records for the island (see appendix). The total species richness is dominated by liverworts, with 158 species, compared to mosses with only 84 species. One hornwort was recorded along the gradient and for convenience it is lumped with the liverworts for all subsequent analyses. Mosses were distributed over the entire gradient, although only one species (*Radulina borbonica*) was recorded at the lowest altitude (350 m), whereas no liverworts were found at 2550 m and only one species (*Radula tabularis*) at 2750 m.

Total bryophyte species richness has a clear humped relationship with altitude, with a very marked maximum at mid-elevation (1350 m) (Figure 1a). The liverworts reached their highest richness at 1150 m (Figure 1b), whereas mosses reached their highest at around 1350 m (Figure 1c). However, liverwort richness differed by only one species between the 1150 m and 1350 m plots.

The results from the ANOVA showed that the effect of the micro habitat (i.e. height on tree where sample was taken) on species richness was insignificant ( $F = 5.1, p > 0.1$ ).

Floristic similarity of the different elevations is shown in Table 1. In general, similarity decreases with distance between two plots. The lowest similarity (highest dissimilarity) occurs between the lowest (350 m) and highest elevation (2750 m), while the two most similar plots are those found at the highest altitude. Species turnover is lower in the upper half of the gradient (above 1350 m).

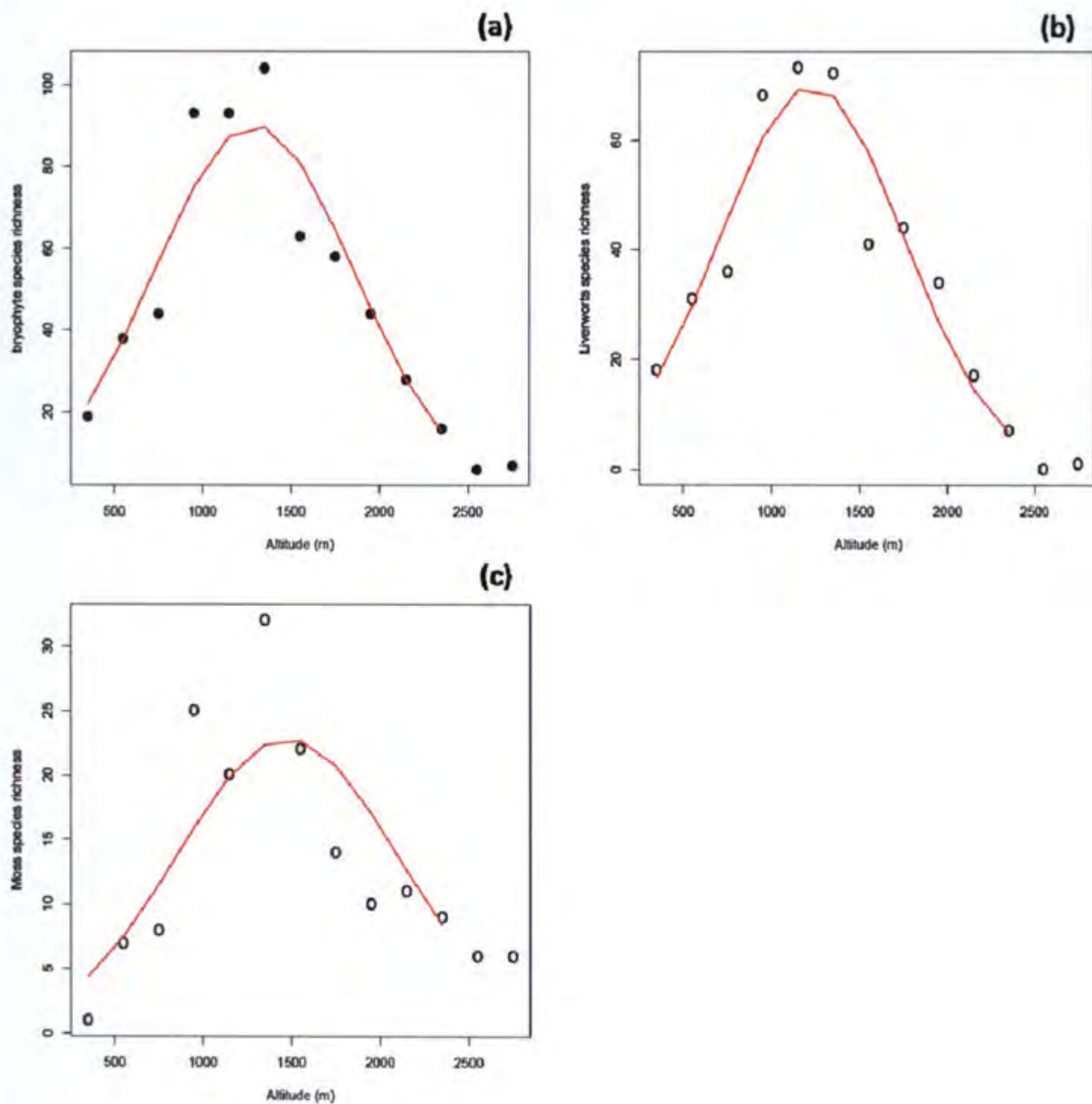


Figure 1. Species richness in relation to altitude. (a) Total bryophyte species richness in relation to altitude. (b) Liverwort species richness in relation to altitude. (c) Moss species richness in relation to altitude. Fitted lines represents a GLM with error distribution treated as Poisson. In all cases curves were significant ( $P < 0.0001$ ).

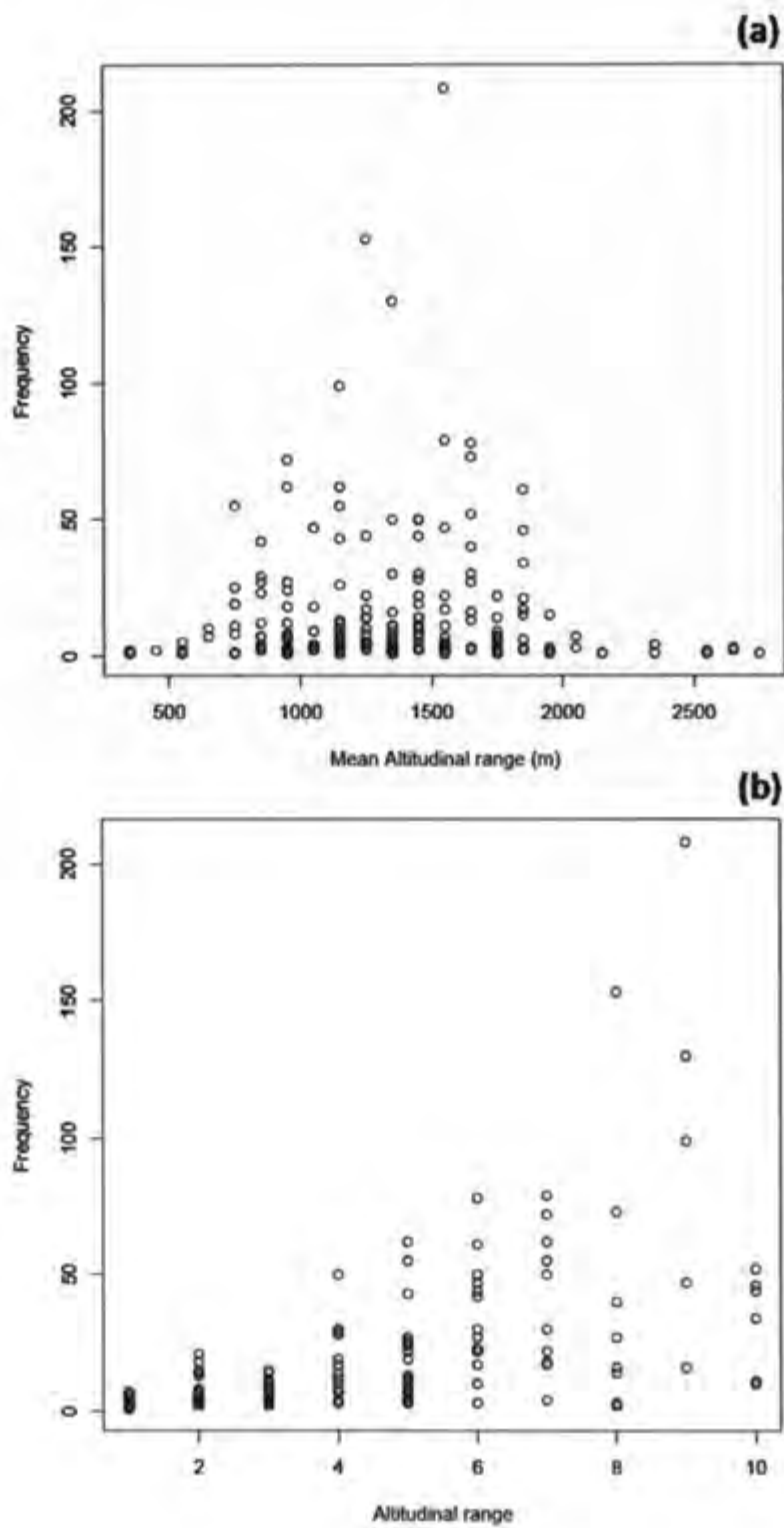
**Table 1.** Floristic similarity between bryophyte communities along the altitudinal gradient. Calculated as 1-jaccard.

	350	550	750	950	1150	1350	1550	1750	1950	2150	2350	2550
550	0.22											
750	0.18	0.30										
950	0.11	0.19	0.27									
1150	0.12	0.21	0.22	0.36								
1350	0.08	0.11	0.14	0.30	0.35							
1550	0.04	0.06	0.15	0.24	0.20	0.30						
1750	0.03	0.07	0.11	0.20	0.18	0.27	0.27					
1950	0.04	0.03	0.10	0.15	0.12	0.15	0.24	0.35				
2150	0.04	0.05	0.07	0.15	0.13	0.15	0.17	0.25	0.38			
2350	0.00	0.02	0.05	0.11	0.08	0.08	0.10	0.10	0.22	0.38		
2550	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.00	0.03	0.03	0.05	
2750	0.00	0.00	0.00	0.02	0.01	0.02	0.01	0.00	0.02	0.06	0.13	0.60

Figures 2a and b show the distribution of rare and common species along the gradient. The majority of species have mean ranges situated between 1000 m and 2000 m in elevation (Figure 2a and 3). The mean altitudinal range of the most common species is centred at mid-elevation, these species also have the largest ranges (2a and b). Rare species appear to be distributed along the entire altitudinal transect. In general, range size increases with commonness of species (2 b).

The prevalent sexual condition for liverworts (Figure 4a) over the entire gradient is dioicy (59 % of species). The only elevation in which monoicous species are better represented is the lowest elevation (350 m). The highest elevation is represented by a single dioicous species. Monoicy is the prevalent sexual condition in mosses and it is especially high at the limits of the gradient (Figure 4b). At only two altitudes (750 m and 950 m) are dioicous mosses equal to or greater in number than monoicous mosses.

Spore size was obtained for 21 of the 30 moss species recorded along the gradient at least four times or more. Spore numbers were calculated for 15 of the 21 species. Spore number showed a hump-shaped relationship with altitude (Figure 5a), with the species producing the largest number of spores at mid-elevation and fewer spores in the upper and lower elevations. The relationship between spore size and altitude (Figure 5b) is the inverse of the relationship noted for spore number and altitude. The largest spores are found in the upper and lower elevations and the smallest at mid-elevations.



**Figure 2.** (a) Frequency of a species along the gradient plotted against mean altitudinal range (m). (b) Frequency of species along the gradient plotted against altitudinal range.



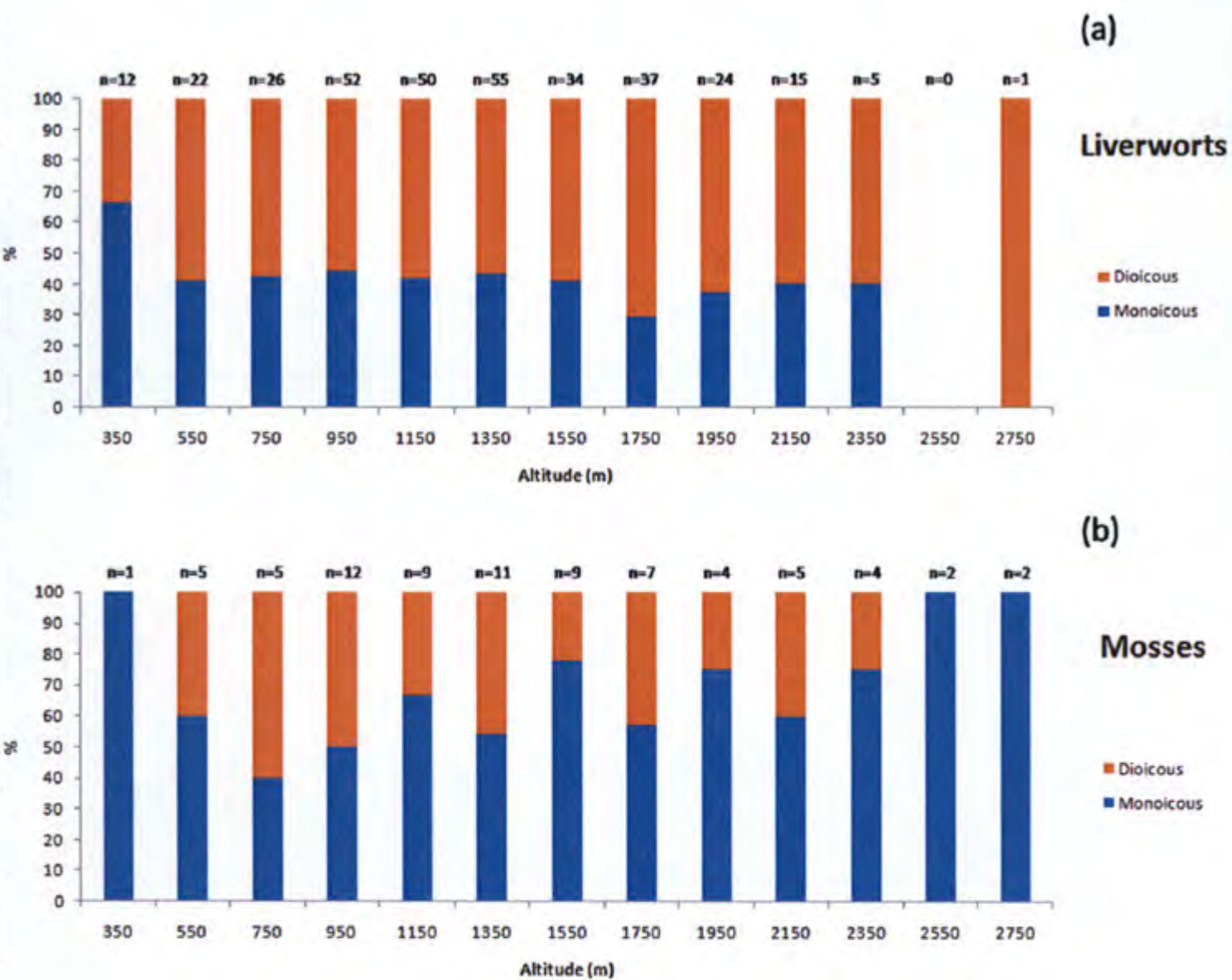
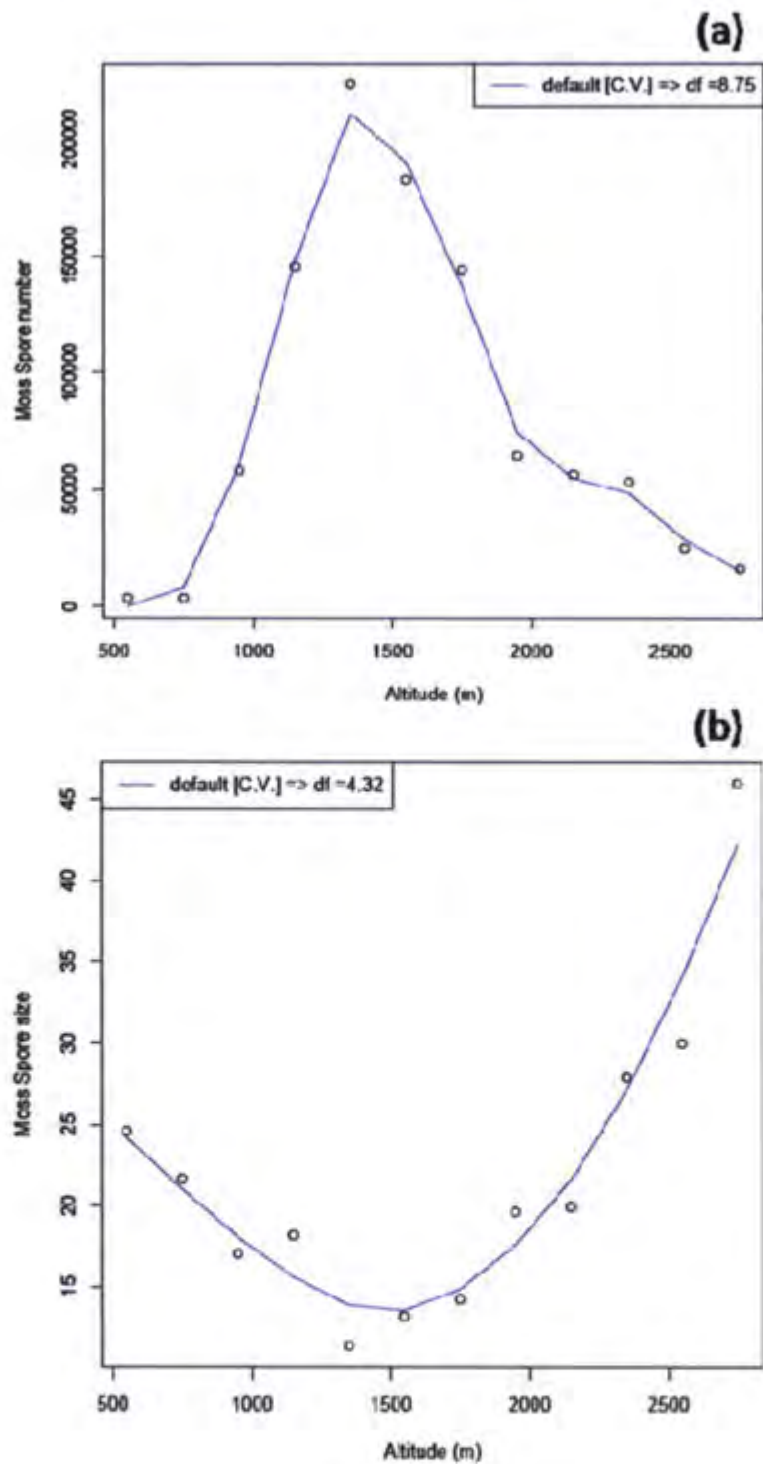


Figure 4. (a) Percentage of monoicous (M) and dioicous (D) liverworts at each altitude. (b) Percentage of monoicous (M) and dioicous (D) mosses at each altitude. Numbers on tops of columns are the total number of species for which data was available.



**Figure 5.** (a) The average number of spores produced by moss species plotted against altitude (m) (b) The average size of moss spores plotted against altitude (m). The fitted lines represent a GAM with cubic smooth spline.

## Discussion

### *Overall Patterns of Species Richness*

Recent work on the distribution of orchids in In La Réunion has revealed a decrease in species richness with altitude (Jacquemyn *et al.*, 2005). In comparison, the number of bryophytes species on a 19 year old lava flow were found to increase with altitude between 250 and 850 m (Ah-Peng *et al.*, 2007).

In the current study, bryophyte species richness was found to vary strongly with altitude. In all cases the patterns show a mid-elevation peak in the number of species, similar to the pattern observed for ferns on the island (Kessler pers. comm.). A hump-shaped relationship of bryophyte richness with altitude has also been found in other areas of the tropics (Gradstein & Pócs, 1989; Wolf, 1993). Recently, Grau *et al.* (2007) reported a unimodal response in the central Himalayas of Nepal which closely matched the distribution of richness in ferns and angiosperms for the region. Hump-shaped patterns of species richness have been repeatedly hypothesized to be due to dispersal of species from lower and higher elevations, resulting in highest overlap of such sink populations at mid-elevations (whereas communities at the extremes of the gradient can only receive immigrants from one direction) (Kessler, 2009). Although, to some, these ideas might seem intuitively appealing, little empirical evidence exists to support these theories. Acebey *et al.*, (2003) proposed that the high species richness was more likely to be explained by a constant supply of moisture which corticolous bryophytes of montane cloud forests experience. Given that bryophyte species richness peaks at the level of the cloud forest (1150-1350 m) on Piton de Neiges, this hypothesis is more appealing.

It is known that hump-shaped patterns of diversity can be driven by a single group of species that display a variation of ranges all centred at the mid-elevation (T.A. Hedderson pers. comm.). Overall patterns in similarity between altitudes suggest that the hump-shaped distribution of richness is due to the presence of different species assemblages over the gradient. This is supported by the fact that over the full range of altitudes many species display very small ranges.

Mosses and liverworts reached peak richness at roughly the same altitude. This is contrary to the findings of Grau et al. (2007) who were also able to show an altitudinal difference in the peak of moss and liverwort species richness. On an oceanic island such patterns could be harder to pick up because a similar range of climates are compressed into a shorter altitudinal range and peaks in richness would be closer than on a continental transect (Ah-Peng, 2007). As a result it is possible that sampling in the current study was not at a fine enough scale to pick up an altitudinal difference in peak richness for the two groups. It is also possible that the patterns which Grau et al (2007) found in a temperate system, might not necessarily apply in tropical or corticolous environments. Additional studies which aim to highlight similar trends and the factors governing them will provide valuable insight for physiological studies on mosses and liverworts.

The distribution of vascular plants is likely to be a significant factor influencing the abundance and distribution of bryophytes at the limits of the gradient, especially at the highest elevations. Similarity in presence and absence of species is higher between mid and upper elevations (between 1350 m and 2750 m) than between low and mid-elevations (between 350 and 1350). Further, the highest elevations (above 2150 m) are all highly similar to each other. This suggests that species turnover in the upper elevations is comparatively less than in the lower elevations and that total species richness in the lower half of the gradient is likely to be much higher than in the top half (richness in bottom half = 262 species and richness in top half = 180 species). Bryophytes are comparatively better adapted to deal with water stress than vascular plants, and it appears that the lack of vascular plants in the upper altitudes precludes the presence of corticolous bryophytes (Goffinet & Shaw, 2009).

Initially it was thought that the microhabitat (height of tree at which sample was collected) may play an important role in affecting the species richness along the gradient, but analysis of the data suggested otherwise. In reviewing the literature it was found that the distribution of species numbers tends to be relatively homogeneous within the corticolous habitat. Only in the highest parts of the tree are species numbers expected to decline due to the increased wind force, light intensity and hence fluctuations in temperature and humidity (Vanderpoorten & Goffinet, 2009).

Much work is being conducted on the factors that affect richness on altitudinal gradients and increasingly it is being realised that these factors are unique between groups of organisms (Badyaev, 1997; Beck & Khen Chey, 2008). The question of whether favourable environmental conditions can be attributed to patterns of richness appears to be largely dependent on the group under study and focus is now towards traits which allow so many species to exist together in a highly competitive environment. The majority of work on bryophytes appears to link patterns of richness, either directly or indirectly, with dispersal traits and mechanisms and recent work suggests that types of reproduction may play a significant role affecting richness on altitudinal gradients (Kessler 2009).

### ***Patterns in rarity and commonness along the gradient***

The most common species along the gradient display the largest altitudinal ranges, and have a mean altitudinal range centred at mid-elevation. However this estimate of mean altitudinal range does not take into account the abundance of the species at a given altitude. This prevents much speculation about the primary habitat, or the altitude at which highest frequency occurs, of the most common species in particular. Common species which are distributed over most of the gradient include the mosses *Schlotheimia badiella* and *Dicranoloma billardierei* and the liverworts *Drepanolejeunea physaefolia* and *Mastigophora diclados*.

There are many types of rarity and species may be rare at different spatial scales. A species may be rare over its entire range or in just a part of it, usually at its distribution limit (extraneous species of Hedderson (1992b)). Rare species can also be locally abundant and occupy a limited distribution or they can exist in very small populations over a very wide distribution (Söderström & Düring, 2005).

Patterns in rarity along the gradient include species that are confined to a small altitudinal range, such as those with a mean ranges at the limits of the gradient and are most likely specialists in their environment. Species restricted to the dry lowland forests (lowest elevation) are comprised solely of liverworts (e.g. *Cololejeunea zenkeri* and *Heteroscyphus dubius*). Rare species with wide ranges (e.g. *Microlejeunea protuberata* sp. Nov.) were also identified along the gradient.

Few studies have tried to associate patterns of rarity and commonness with variation in life history traits (Söderstrom and During, 2005) and those that have done so tend to identify sexuality and spore production as of particular importance. Analysis of correlations in the British flora by Longton (1992b) and Laaka-Lindberg *et al.* (2000b) showed that species not producing sporophytes were much more often rare than species that did. This applies to dioicous species in particular because of the presence of many single sex populations. Interestingly, among the sporophyte-producing species more monoicous than dioicous species were found to be rare, and this is attributable to the high levels of asexual reproductive effort in dioicous species (Söderstrom and During, 2005).

The data for rarity and commonness presented in this study are extremely detailed (based on an excess of 3132 identifications for corticolous species only) and in combination with a much more complete data set of corresponding life history information it could contribute greatly to an understanding of how life history traits influence the distribution and success of species in the environment.

### ***Variation in sexuality along the gradient***

The extent to which monoicous and dioicous species reproduce both sexually and asexually is largely unknown for La Reunion, but, it is widely accepted that dioicous species rely to a greater extent on asexual reproduction as a means to ensure survival when the opposite sex is absent, whereas monoicous species rely more on sexual reproduction (Hedderon & Longton, 1995; Laaka-Lindberg *et al.*, 2000b). It has been estimated that more than half of all moss taxa and approximately two thirds of liverworts worldwide are dioicous (Wyatt, 1982). The prevalence of dioicous liverworts (59%) found along the gradient is consistent with worldwide estimates; although slightly lower than would be expected, these results don't seem unlikely given that the chance of a dioicous species dispersing to, and persisting on an island is probably much lower than for a monoicous species. This assumes that dioicous species will be poorer long distance dispersers due to infrequent spore production and that they will suffer an increased risk of extinction if only one sex is present.

The presence of single liverwort at the highest elevation (2750 m) is likely to be a chance occurrence, and the fact that it is dioicous is not regarded to be of any ecological significance. At the lowest altitude (350 m), which is characterized by relatively patchy, low-density forest, there is a shift to monoicy as the dominant sexual state. This provides support for recent findings by Löbel *et al.* (2008), which suggest that species reproducing predominantly by asexual means (dioicous) may drastically decline as habitat 'patchiness' increases. To our knowledge these are the first results from an altitudinal gradient that support their findings.

In mosses the pattern is comparatively less clear, preventing much speculation on reasons for the prevailing sexual condition at each altitude. The expected level of dioicy is lower than expected (38%) and is probably due to the same reason as mentioned above for liverworts. One pattern that does stand out is the increased tendency for the monoicous condition at the upper most elevations. The upper elevations are characterised by having almost no trees (i.e. a highly fragmented habitat, see appendix) and a generally harsher environment. Under such conditions the probability of establishing in a suitable patch (i.e. on a tree) is extremely low. Given that a species is able to find a suitable patch it then has to persist in the environment. Monoicy in combination with the production of large spores (e.g. *Ulota fulva* at 2350 and 2750 m), and the benefits which they confer in terms of survival and faster juvenile growth rates, could help to explain how species persist in these environments (During, 1979). A similar situation exists in which many ephemeral taxa and taxa adapted to harsh and unpredictable environments are monoicous, allowing them to complete their life cycle and produce spores during favourable conditions (Longton, 1988). The problem with being dioicous in such an environment is that both male and female plants would need to colonize the same area on a tree for sexual reproduction to occur and the odds of this are extremely low. Asexual propagules would not help dioicous species persist in harsh environments as they are not suited to survive periods of adverse conditions. Additionally, the distance between suitable habitat patches should preclude effective dispersal and establishment of asexual propagules due to their large size and subsequent short dispersal distances (During, 1979; Longton & Schuster, 1983).

### ***Altitudinal variation in Moss Spore size and Number***

The species sampled along the gradient showed a clear trade-off between spore size and number. The size and number of spores produced appears to be significantly related to the altitude at which species occur and are expected to confer strategic advantages in these different environments.

Species producing large numbers of small spores (e.g. *Campylopus flexuosus* var. *flexuosus*, ~ 700 000 spores per capsule) were most frequently found at mid-elevation where competitive interactions are expected to be the highest due to the large number of species present. In the corticolous environment the probability of a single spore establishing in a habitable patch (e.g. on the trunk of a tree) is extremely low and the production of large numbers of spores is essential for effective dispersal and an increased likelihood at establishment. Spore size is not only relevant in relation to the number of spores that a sporophyte can produce. Miles and Longton (1990) showed that probable dispersal distance rapidly decreases for spores >25  $\mu\text{m}$ . Small spores thus offer the possibility of large spore numbers and long-range dispersal distance, thereby maximizing a species chance at finding and establishing in open patches. Disadvantages of small spore size probably include, among other things, a decreased juvenile growth rate. However, at mid-elevation this probably has little influence on whether a juvenile makes it to a mature plant, as the relative persistence of favourable conditions means that there is no urgency to establish quickly and produce sporophytes.

In comparison, the conditions experienced at upper and lower elevations appear to favour species that produce fewer large spores (e.g. *Ulota fulva*, ~ 3 000 spores per capsule). Apportioning available resources among a few but very large spores presumably increases both spore survival and juvenile growth rates. The associated reductions in spore number and dispersability would probably be outweighed by the fact that appropriate habitat patches are more likely to occur in the same vicinity (Hedderson and Longton, 1995). Species like *Ulota fulva* are probably quite effective at establishing on parts of the same tree as their spores have an increased tendency to be dispersed by gravity and thus become lodged in between crevices of the bark, waiting for favourable conditions. The scarcity of trees and presence of less

favourable conditions in the upper elevations are consistent with this theory. Species producing small spores are likely to be precluded from upper elevations because of a reduced ability to establish in harsher environments and due to the tendency of their spores to be quickly carried away from the few favourable sites.

The importance of large spores at lower altitudes appears to be less pronounced while factors precluding species with many small spores are less apparent, they are probably linked with a lower survival probability in the relatively more xeric habitat of lowland forests.

Although this study did not examine patterns of asexual propagule production, many studies have noted its relation to production of spores and to sexuality of the plants (During, 1979; Hedderson & Longton, 1995; Hedderson, 1996). Asexual reproduction is possible via production of specialized asexual diaspores (gemmae, gemmae-like branches), via clonal growth or by fragmentation (During *et al.*, 1987; Laaka-Lindberg *et al.*, 2003). Most asexual diaspores are substantially larger than spores, generally possessing much shorter dispersal distances as a result but higher rates of establishment (Löbel and Rydin 2009). Recent work by Kessler (2009) suggests that production of asexual propagules may play an important role in the structuring of species richness in relation to altitude.

## Conclusion

The results presented in this study provide a preliminary look at the relationship between altitude and the variation in a few but important life history traits for bryophytes on a tropical island. Knowledge of how bryophytes are adapted to their environment with regard to survival and reproductive strategies is paramount for a general understanding of the factors related to trends in richness, and those that affect structuring of communities.

The distribution of richness along the gradient although largely a result of the ideal climate conditions at mid elevation and distribution of vascular plants must also be associated, to a certain extent, with evolutionary constraints and the variation in life history strategies of corticolous species. One such strategy, which is increasingly being invoked to explain the composition of metapopulations, may be the type and degree of reproductive effort.

Thus, variation in spore size and spore number along the gradient may largely be attributable to the interaction between competition at mid-elevation and the need for greater parent-offspring investment at the higher elevations. The clear lack of basic life history data for bryophytes is evident and there is an important need for such data to be recorded. Additional data on spore size and the relative frequency of sexual and asexual reproduction could provide a means to ask increasingly detailed questions regarding the altitudinal variation in reproductive traits, their conferred benefits and associated trade-offs.

A further understanding of the variation in life history traits may greatly increase our knowledge of why some species are rare, their range and additional habitats in which they could be found. This has important implications for conservation planning and practice, especially on La Réunion, where many of the low elevation sites are under threat of development.

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## Appendix



2950 m



(1) 2750 m

Subalpine shrubland

26/03/2008

GPS:

Plot 1: 21°06'28S; 55°30'22 E

Plot 2: 21°05'56 S; 55°30'23 E



(2) 2550, (3) 2350 m

Shrubland

20/03/2008

GPS, 2350 m:

Plot 1: 21°05'56 S; 55°30'22 E

Plot 2: 21°05'56 S; 55°30'23 E

GPS, 2550 m

Plot 1: 21°06'33 S; 55°30'22 E

Plot 2: 21°05'56 S; 55°30'23 E



(4) 2150

*Philippia* thickets

29/03/2008

GPS:

Plot 1: 21°05'17 S; 55°30'16 E

Plot 2: 21°05'15 S; 55°31'20 E



(5) 1950 m

*Philipia* thickets

29/03/2008

GPS:

Plot 1: 21°05'17 S ; 55°30'16 E

Plot 2: 21°05'15 S; 55°31'20 E



(6) 1750 m

Mountain windward rainforest

20/03/2008

GPS:

Plot 1: 21°04'42 S; 55°31'42 E

Plot 2 : 21°04'42 S; 55°31'42 E



(7) Sentier de l'Ecole Normale, 1550 m

*Accacia heterophylla* mountain forest

27/03/2008

GPS:

Plot 1: 21°04'33 S; 55°32'36 E

Plot 2: 21°04'33 S; 55°32'26 E



**(8)** Sentier de la Rivière, 1350 m

Submountain windward forest

27/03/2008

GPS:

Plot 1: 21°06'23" S; 55°34'36 E

Plot 2 : 21°05'56 S; 55°30'23" E



**(9)** Takamaka, 1150 m

Submountain windward forest

28/03/2008

GPS:

Plot 1: 21°05'50 S; 55°35'19 E

Plot 2: 21°05'51 S; 55°35'19 E



**(10)** Plaine des Palmistes, 950 m  
Permanent plot of the University

*Pandanus* wet thickets

22/03/2008

GPS:

Plot 1: 21°06'58 S; 55°38'21 E

Plot 2: 21°06'57 S; 55°38'41 E



**(11)** Plaines des Lianes, 750 m

Lowland rainforest

19/03/2008

GPS:

Plot 1: 21°02'00 S; 55°36'32 E

Plot 2: 21°02'00 S; 55°36'30 E



**(12)** Grand Etang, 550 m

Lowland rainforest

23/03/2008

GPS:

Plot 1: 21°05'46 S; 55°39'62 E

Plot 2 : 21°05'46 S; 55°39'02 E



**(13)** La Caroline, 350 m

Lowland rainforest

20/03/2008

GPS:

Plot 1: 21°00,40 S; 55°38'19 E

Plot 2: 21°00'40 S; 55°38'11E

Abb.	Bryophyte species	Family	350 m	550 m	750 m	950 m	115 0 m	135 0 m	155 0 m	175 0 m	195 0 m	215 0 m	235 0 m	255 0 m	275 0 m	Tot. Occ.
acem	<i>Acrolejeunea emergens</i> var. <i>emergens</i> (Mitt.) Steph.	Lejeuneaceae	0	0	0	1	0	0	0	0	0	0	0	0	0	1
acme	<i>Acroporium megasporum</i> (Duby) M.F. Fleisch.	Sematophyllaceae	0	19	13	7	4	0	4	0	0	0	0	0	0	47
adde	<i>Adelanthus decipiens</i> (Hook.) Mitt.	Adelanthaceae	0	0	0	4	8	7	0	7	4	0	0	0	0	30
aesu	<i>Acrobryidium subpiligerum</i> var. <i>majus</i> (Renauld & Cardot) Wijk & Margad.	Meteoriaceae	0	4	0	4	0	0	0	0	0	0	0	0	0	8
amdi	<i>Amazoopsis diplopoda</i> (Poes) J.J. Engel et G.L.S. Merr.	Lepidoziaceae	0	0	0	0	2	0	0	0	0	0	0	0	0	2
anau	<i>Anastrophyllum auritum</i> (Lehm.) Steph.	Jungermanniaceae	0	0	0	0	0	0	0	2	1	0	0	0	0	3
anmi	<i>Anastrophyllum minutum</i> (Schreb.) R.M. Schust.*	Jungermanniaceae	0	0	0	0	2	0	0	0	1	0	0	0	0	3
anpl	<i>Anastrophyllum piligerum</i> (Reinw.; Blume & Nees) Steph.	Jungermanniaceae	0	0	0	0	0	0	0	1	5	0	0	0	0	6
anab	<i>Andrewsianthus aberrans</i> (Nees & Mont.) Grolle	Jungermanniaceae	0	0	1	0	0	0	1	0	2	0	0	0	0	4
anbl	<i>Andrewsianthus cf. bilobus</i> (Mitt.) Grolle *	Jungermanniaceae	0	0	2	2	0	1	2	1	0	6	0	0	0	14
anla	<i>Aneura latissima</i> Spruce	Aneuraceae	0	0	0	0	0	0	0	1	1	0	0	0	0	2
bade	<i>Bazzania decrescens</i> (Lehm. & Lindenb.) Trevis.	Lepidoziaceae	0	1	5	9	18	29	0	0	0	0	0	0	0	62
bade m	<i>Bazzania decrescens</i> subsp. <i>molleri</i> (Steph.) E.W. Jones	Lepidoziaceae	0	0	0	0	1	1	0	5	0	0	0	0	0	7
bama	<i>Bazzania mascarena</i> (Steph.) Herzog	Lepidoziaceae	0	0	0	10	2	6	21	21	12	7	0	0	0	79
banl	<i>Bazzania nitida</i> (F. Weber) Grolle	Lepidoziaceae	0	4	5	3	21	14	1	14	0	0	0	0	0	62
bapr	<i>Bazzania praeurupta</i> (Reinw., Blume & Nees) Trevis.	Lepidoziaceae	0	0	0	1	6	7	1	28	1	0	0	0	0	44
baro	<i>Bazzania roccatii</i> Gola	Lepidoziaceae	0	0	9	0	0	2	1	0	0	0	0	0	0	12

























Moss Species	Family	Monocious	Diocious	Mean spore	Capsule length	Capsule width	Spore number
<i>Acroporium megasporum</i> (Duby) M.Fleisch.	Sematophyllaceae	1	0	21	0.4	0.3	3674
<i>Aerobryidium subpiligerum</i> var. <i>majus</i> (Renauld & Cardot) Wijk & Margad.	Meteoriaceae	1	0	NA			
<i>Brachymerium eurychelium</i> Besch.	Bryaceae	NA	NA	NA			
<i>Calymperes palisotii</i> Schwägr.	Calymperaceae	0	1	21			
<i>Campylopus arctocarpus</i> ssp. <i>maderassus</i> (Besch.) J.-P.Frahm.	Dicranaceae	0	1	12	1.25	0.32	70013
<i>Campylopus aureonitens</i> (Müll.Hal.) A. Jaeger	Dicranaceae	NA	NA	15			
<i>Campylopus crateris</i> Besch.	Dicranaceae	0	0	12	1.8	0.64	
<i>Campylopus flexuosus</i> var. <i>flexuosus</i> (Hedw.) Brid.	Dicranaceae	0	1	14	2	1	688905
<i>Campylopus jamesonii</i> (Hook.) A. Jaeger	Dicranaceae	NA	NA	NA			
<i>Campylopus robillardii</i> Besch.	Dicranaceae	0	0	10	1.5	0.4	
<i>Campylopus thwaitesii</i> (Mitt.) A. Jaeger	Dicranaceae	0	1	10	1	0.6	340264
<i>Cyclodictyon borbonicum</i> (Besch.) Broth.	Ptilotrichaceae	NA	NA	NA			
<i>Cyclodictyon brevifolium</i> Broth.	Ptilotrichaceae	NA	NA	15	1.6	0.5	84970
<i>Daltonia angustifolia</i> var. <i>angustifolia</i> Dozy & Molk.	Daltoniaceae	1	0	11.25	0.8	0.4	
<i>Daltonia latimarginata</i> Besch.	Daltoniaceae	NA	NA	NA	1	0.75	
<i>Dicranoloma billardierei</i> (Brid.) Paris	Dicranaceae	1	0	16	1.5	0.5	86534
<i>Dicranoloma billardierei</i> var. <i>scopareolium</i> (Müll.Hal.) Thér.	Dicranaceae	NA	NA	NA			
<i>Dicranoloma borbonicum</i> Renauld & Cardot	Dicranaceae	NA	NA	NA			
<i>Ectropothecium regulare</i> (Brid.) A. Jaeger	Hypnaceae	NA	NA	NA			
<i>Ectropothecium valentinii</i> Besch.	Hypnaceae	NA	NA	NA			
<i>Fissidens asplenioides</i> Hedw.	Fissidentaceae	NA	NA	NA			
<i>Fissidens sciophyllus</i> fo. <i>sciophyllus</i> Mitt.	Fissidentaceae	NA	NA	14	0.35	0.1	
<i>Holomitrium borbonicum</i> Besch.	Dicranaceae	1	0	11.5	2	0.25	77684
<i>Holomitrium cylindraceum</i> var. <i>cylindraceum</i> (P.Beauv.) Wijk & Margad.	Dicranaceae	NA	NA	15.5			

<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i> Hedw.	Hyphaceae	NA	15.5	2	0.35
<i>Isopterygium cirinellum</i> Renauld & Cardot	Hyphaceae	NA	NA		
<i>Jaegerina solitaria</i> (Brid.) A.Jaeger	Pterobryaceae	0	24	1	
<i>Jaegerina solitaria</i> var. <i>ramosa</i> Besch.	Pterobryaceae	NA	NA		
<i>Lepidopilidium cespitosum</i> (Besch.) Broth.	Pilotrichaceae	NA	NA		
<i>Lepidopilidium hirsutum</i> Besch.	Pilotrichaceae	NA	NA		
<i>Leptodontium flexifolium</i> (Dicks.) Hampe	Pottiaceae	NA	17.5	1	0.25
<i>Leucobryum cf. boryanum</i> Besch.	Leucobryaceae	NA	NA		
<i>Leucobryum cf. isleanum</i> Besch.	Leucobryaceae	NA	NA		
<i>Leucobryum mayottense</i> Cardot	Leucobryaceae	NA	NA		
<i>Leucoloma bifidum</i> (Brid.) Brid.	Dicranaceae	0	21	1	0.7
<i>Leucoloma candidulum</i> Besch.	Dicranaceae	NA	NA		
<i>Leucoloma capillifolium</i> Renauld	Dicranaceae	0	24.5	1	
<i>Leucoloma cinclidotioides</i> Besch.	Dicranaceae	NA	NA		
<i>Leucoloma delicatum</i> Renauld	Dicranaceae	NA	NA		
<i>Leucoloma grandidierti</i> Renauld & Cardot	Dicranaceae	NA	NA		
<i>Leucoloma lepervancheri</i> Besch.	Dicranaceae	1	NA	0	
<i>Leucoloma seychellense</i> Besch.	Dicranaceae	NA	24.5		
<i>Leucophanes angustifolium</i> Renauld & Cardot	Calypteroaceae	NA	17.5	2	0.75
<i>Macrocoma tenuis</i> ssp. <i>tenuis</i> (Hook. & Grev.) Vitt	Orthotrichaceae	NA	38	1.3	0.9
<i>Macrohymenium acidodon</i> (Mont.) Dozy & Molk.	Sematophyllaceae	NA	17.5		
<i>Macromitrium mauritianum</i> Schwägr.	Orthotrichaceae	NA	25	0.8	0.6
<i>Macromitrium microstomum</i> (Hook. & Grev.) Schwägr.	Orthotrichaceae	1	30	2	0.6
<i>Macromitrium pallidum</i> (P.Beauv.) Wijk & Margad.	Orthotrichaceae	NA	NA	0.9	0.5
<i>Macromitrium rufescens</i> Besch.	Orthotrichaceae	NA	NA		
<i>Macromitrium serpens</i> (Bruch ex Hook. & Grev.) Brid.	Orthotrichaceae	NA	35	1	0.76
<i>Mittenothamnium limosum</i> (Besch.) Cardot	Hyphaceae	NA	NA		

<i>Papillidiopsis complanata</i> (Dixon) W.R.Buck & B.C.Tan	Sematophyllaceae	1	0	15.5	1		15863
<i>Polytrichum commune</i> var. <i>commune</i> Hedw.	Polytrichaceae	NA	NA	6.5	2.2	1.6	
<i>Porotrichum elongatum</i> (Welw. & DuBy) A. Gepp	Neckeraceae	NA	NA	12.5			
<i>Porotrichum madagassum</i> Kiaer ex Besch.	Neckeraceae	NA	NA	19			
<i>Porotrichum usagarum</i> Mitt.	Neckeraceae	NA	NA	13.5			
<i>Pyrrhobryum spiniforme</i> (Hedw.) Mitt.	Rhizogoniaceae	1	0	16	1.8	0.6	149530
<i>Pyrrhobryum spiniforme</i> var. <i>brevifolium</i> (Besch.) Manuel	Rhizogoniaceae	NA	NA	NA			
<i>Racomitrium membranaceum</i> (Mitt.) Paris	Grimmiaceae	NA	NA	11	0.9	0.4	
<i>Racopilum africanum</i> Mitt.	Racopilaceae	NA	NA	NA			
<i>Radulina borbonica</i> (Bél.) W.R.Buck	Sematophyllaceae	1	0	NA	0.5	0.1	
<i>Rhaphidorrhynchium crispans</i> (Besch.) Broth.	Sematophyllaceae	NA	NA	NA			
<i>Rhaphidorrhynchium rubricaula</i> (Besch.) Broth.	Sematophyllaceae	NA	NA	NA			
<i>Schlotheimia angulosa</i> P.Beauv.	Orthotrichaceae	NA	NA	NA			
<i>Schlotheimia badiella</i> Besch.	Orthotrichaceae	NA	NA	27.5	1.85	0.38	12141
<i>Schlotheimia microcarpa</i> Geh.	Orthotrichaceae	NA	NA	25	0.9	0.3	
<i>Schlotheimia squarrosa</i> Brid.	Orthotrichaceae	NA	NA	25	1	0.3	5444
<i>Sematophyllum crassiusculum</i> (Brid.) Broth.	Sematophyllaceae	NA	NA	NA			
<i>Sematophyllum schimperi</i> (Besch.) Broth.	Sematophyllaceae	NA	NA	NA			
<i>Sematophyllum subpinnatum</i> (Brid.) E. Britton	Sematophyllaceae	1	0	19	1.5/0.1	0.44/0.05	40017
<i>Serpotortella cyrtophylla</i> (Besch.) W.D.Reese & R.H.Zander	Serpotortelliaceae	NA	NA	NA			
<i>Sphagnum tumidulum</i> var. <i>tumidulum</i> Besch.	Sphagnaceae	2	0	NA			
<i>Syrrhopodon dimorphophyllum</i> L.T.Ellis	Calymperaceae	NA	NA	NA			

