



Functional Diversity of Subalpine Bryophyte Communities in an Oceanic Island (La Réunion)

Authors: Ah-Peng, Claudine, Flores, Olivier, Wilding, Nicholas, Bardat, Jacques, Marline, Lovanomanjanahary, et al.

Source: Arctic, Antarctic, and Alpine Research, 46(4) : 841-851

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: <https://doi.org/10.1657/1938-4246-46.4.841>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Functional diversity of subalpine bryophyte communities in an oceanic island (La Réunion)

Claudine Ah-Peng*‡#

Olivier Flores‡

Nicholas Wilding*

Jacques Bardat§

Lovanomanjanahary

Marline*

Terry A. J. Hedderson* and

Dominique Strasberg†

*Department of Biological Sciences,
University of Cape Town, Private Bag
X3, 7701 Rondebosch, South Africa

‡University of La Réunion, UMR
PVBMT, 15 Avenue René Cassin,
97715 Saint-Denis, France

‡CIRAD, UMR PVBMT, Pôle de
Protection des Plantes, 7 Chemin de
l'IRAT, 97410 Saint-Pierre, France

§Muséum National d'Histoire
Naturelle, Institut de Systématique,
Evolution et Biodiversité, UMR CNRS-

7205, 57 Rue Cuvier, B.P.39, 75 231
Paris Cedex 05, France

#Corresponding author:

claudine.ahpeng@gmail.com

Abstract

Increasing temperature imperils worldwide tropical subalpine and alpine ecosystems with the threat of mountaintop extinctions and a subsequent loss of biodiversity and ecosystem functions. This paper provides a first assessment of functional diversity along a high climatic gradient for bryophytes, which represent a major plant compartment in these ecosystems. The present study takes place on the highlands of the Piton des Neiges volcano, the highest summit of La Réunion Island (Western Indian Ocean). We find a relatively high species richness of bryophytes in these subalpine habitats, with a peak of diversity at 2750 m for the ground-dwelling community. We report a strong linear relationship between functional diversity and species richness for epiphytes. Within the same plant group, the relationship between functional richness, based on eight traits, and elevation differed between the ground-dwelling and epiphytic communities, suggesting that different processes may structure bryophyte species assemblages along this short subalpine climatic gradient. Higher functional redundancy in ground-dwelling bryophyte assemblages indicates that this community may be more robust than epiphytic bryophytes to disturbances in these subalpine ecosystems.

DOI: <http://dx.doi.org/10.1657/1938-4246-46.4.841>

Introduction

Despite a general consensus that emerged in the late 1980s supporting anthropogenic global warming, most conservation biologists saw climate change in the tropics as a much less immediate threat than deforestation, logging, and hunting (Corlett, 2012). There has since been a general and rapid shift of opinion among tropical biologists, with widespread recognition that climate is already affecting geographic ranges of both plant and animal species (Colwell et al., 2008; Corlett, 2012). Potential effects of climate change on tropical systems include biodiversity loss and change in ecosystem processes, both of which could affect their integrity. Although difficult to predict due to a shortage of data, such effects may be critical on oceanic islands, which have accumulated diverse and specific local species assemblages. Such islands often harbor a high proportion of endemic species, which are therefore at threat in the face of habitat alteration and/or species invasions (Caujapé-Castells et al., 2010). In particular, young, typically high volcanic islands comprise a range of habitats including tropical subalpine and alpine systems. These high-elevation habitats have received little attention and are underrepresented in the literature. This situation arises from difficulties in reaching remote archipelagoes, and from problems with undertaking fieldwork in humid, tropical alpine conditions (Körner, 2003).

Subalpine bryophyte communities have received little attention in the tropics, as most explorations have focused on luxuriant cloud forests where the biomass and diversity of these non-vas-

cular plants peak. However, because bryophytes are poikilohydric organisms with varying degrees of desiccation tolerance, they also grow at high altitudes and their elevational ranges often exceed those of vascular plants. They are dominant in high altitude ecosystems (Theurillat et al., 2003; Robinson and Waterman, 2014), where they account for a large proportion of primary production. For instance, in alpine shrub meadows on the Tibetan plateau, bryophyte species contribute up to 35% of primary production (Li and Qi, 1993). Although small and apparently simple, bryophytes have numerous, although still little studied, adaptations that enable them to survive and maintain populations in harsh conditions. The application of functional ecological concepts (widely used in vascular plant studies) to bryophytes remains an open, and potentially very productive, field of research. In particular, key functional traits that enable these small, non-vascular plants to live in extreme climatic situations have not yet been studied in the tropics.

Functional diversity (FD), a measure of the variety of niches or functions within a system, is thought to be a key driver of ecosystem processes, ecosystem resilience to environmental change and ecosystem services (de Bello et al., 2010). It is an important tool in community ecology because it captures information on biological functions that is absent in measures of species diversity (Poos et al., 2009), allowing a better understanding of community assembly rules and mechanisms of species coexistence. In theory, two main processes control community assembly: niche filtering and limiting similarity. From the former perspective, environmental factors act as niche filters, selecting species that will be more

similar than expected by chance. Local species assemblages are thus expected to be redundant, with a relatively narrow spectrum of traits represented in the community (Zobel, 1997). Conversely, limiting similarity (MacArthur and Levins, 1967) and associated competitive exclusion concepts (Hardin, 1960) assume that functionally complementary species lead to low redundancy and thus can stably coexist in the face of strong interspecific competition. Recent studies suggest that in natural ecosystems these processes co-occur or occur sequentially along an environmental gradient and will influence the relationship between species richness and functional diversity (Mouchet et al., 2010). Consequently, species assemblages and the level of redundancy among species are expected to derive from the relative strengths of niche filtering versus limiting similarity (Mouillot et al., 2007; Mouchet et al., 2010). In subalpine and alpine ecosystems, niche filtering is expected to be the major mechanism, as abiotic conditions are less favorable for plant life, leading to a decrease in competitive intensity (Weiher and Keddy, 1995). Little is known about the relationship between species richness and functional diversity for most organisms, in most ecosystems (Naeem, 2002; Micheli and Halpern, 2005). Recent studies have focused on marine, lacustrine, river, and terrestrial assemblages along disturbed and undisturbed gradients, but only a few have explored the patterns of functional diversity across major geographic gradients such as the elevational and latitudinal gradient (Stevens et al., 2003).

In this paper, we analyze bryophyte diversity and distribution within two main habitats, tree trunks and ground on the highest summit of La Réunion (Piton des Neiges volcano, 3069 m). For the first time, we explore the species richness and the associated growth forms of these highland bryophyte communities, along with their functional diversity based on traits thought to be important for resource use and adaptation to harsh conditions in subalpine ecosystems. The questions we address are: (1) How is bryophyte richness partitioned by elevation and between microhabitats? (2) What is the relationship between species diversity and functional diversity in bryophyte assemblages along a subalpine tropical island gradient? (3) Do two different bryophyte communities (ground- and trunk-dwelling) show similar functional diversity along this gradient?

Material and Methods

STUDY AREA AND FLORA

La Réunion island is, along with Mauritius and Rodrigues, part of the Mascarene archipelago in the Western Indian Ocean. La Réunion (55°39'E; 21°00'S), at 2512 km², is the largest and highest island of the archipelago. Though largely created by the dormant Piton des Neiges volcano (3069 m), the southeast of the island currently hosts an active volcano, the Piton de La Fournaise (2631 m), which erupts regularly. The island is remarkable for its high level of well-preserved biodiversity: 32% of the native vegetation is still well conserved due to a highly variable topography (Ah-Peng et al., 2007) that restricts agriculture and urbanization, and since 2007 this area has been under the protection of a national park.

The climate is predominantly tropical with summer rainfall from November to April and a cooler drier season from June to September. Mean annual temperature varies from 24 °C along the coastline to 12 °C at around 2000 m. There is a steep temperature gradient with altitude with a decrease of 0.7 to 0.8 °C every 100 m. The island receives most rainfall from the moist trade winds on the eastern side with a maximum of 18,000 mm yr⁻¹ at 1600 m (Barcelo, 1996). In the alpine and subalpine habitats, climate is quite vari-

able (Lacoste and Picot, 2011): mean annual temperature ranges from 6 to 8 °C, with extremes of +15 to -2 °C. Solar radiation on the Piton des Neiges can reach 1700 kWh m⁻². Annual mean precipitation varies from 2 m (western slope) to 3.5 m (eastern slope).

The subalpine habitat studied here covers 14,744 ha (Strasberg et al., 2005). Vascular plant species richness is 206 species with 47% endemic (32% endemic to Réunion and 15% to the Mascarenes; Lacoste and Picot, 2011). In addition 78% of the 32 described subalpine habitats are endemic to the island. They are therefore considered of high interest for setting conservation priorities (Strasberg et al., 2005). From the treeline to the summit, the vegetation is continuous low heathland comprising mainly *Stoebe passerinoides* (Lam.) Willd., *Phyllica nitida* Lam., *Erica reunionensis* E.G.H. Oliv., *Hypericum lanceolatum* var. *angustifolium* (Lam.) N. Robson, *Hubertia tomentosa* var. *conyzoides* (Bory) C. Jeffrey, and *Faujasia squamosa* (Bory) C. Jeffrey. Human disturbance and alien species cover remain low at these elevations.

The La Réunion bryophyte flora consists of 831 species, including 504 moss species, 322 liverworts, and 5 hornworts (Ah-Peng et al., 2010; Ah-Peng et al., 2012). It is the richest island in the Mascarene archipelago for bryophytes, mainly due to the broad elevational gradient and the large variety of well-conserved habitats.

STUDY SYSTEM: TRANSECT ALONG THE PITON DES NEIGES VOLCANO

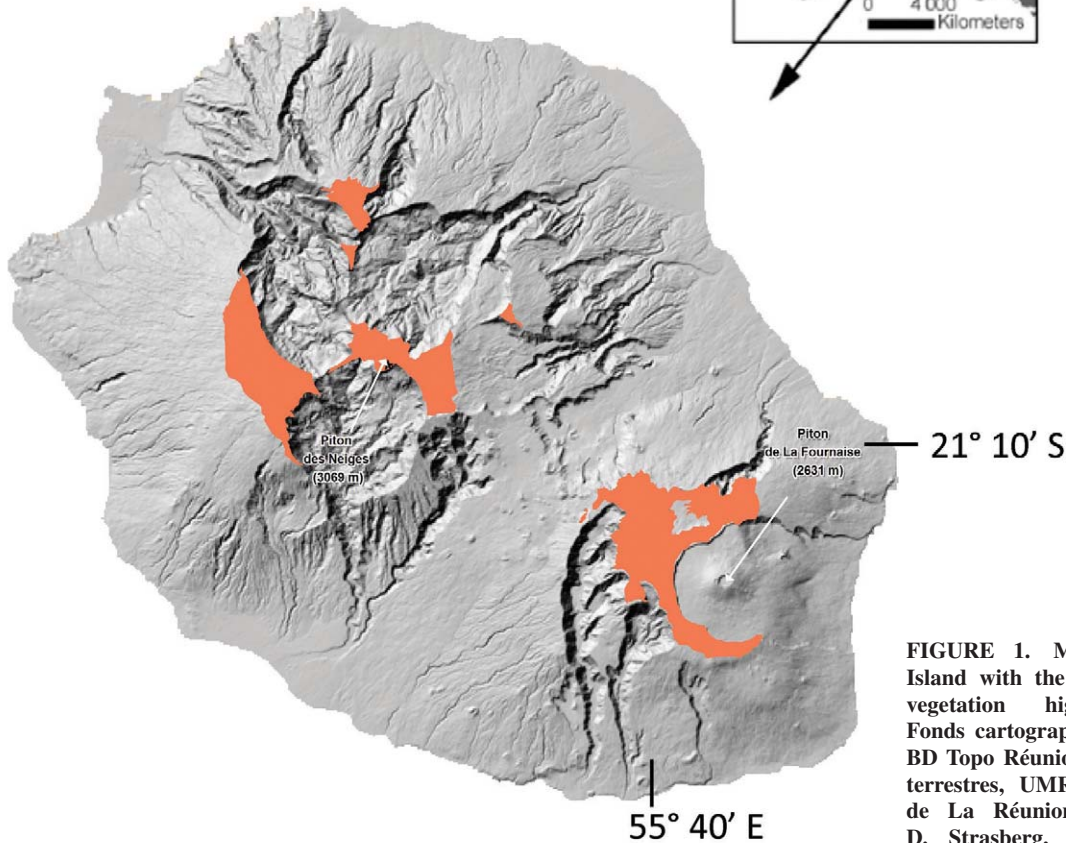
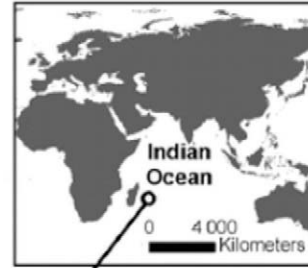
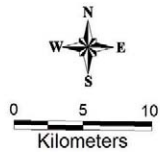
In 2008, a transect from 2150 to 3050 m a.s.l. was set up on the Eastern side of the Piton des Neiges (Fig. 1). At 200 m intervals from 2150 to 2950 m (5 sites), as well as at a site at 3050 m (a 100 m elevational step), we set up two 10 × 10 m plots. Within each plot, three quadrats of 2 × 2 m were chosen randomly. In each quadrat, three 5 × 10 cm samples of bryophytes were selected randomly from each of six microhabitats when present: on three trees (trunk-dwelling community) at 3 different heights (0–50 cm, 0.5–1 m, and 1–2 m), on the soil (terricolous), humus (humicolous), and rock (rupicolous) for the ground-dwelling community. We merged these three ground-dwelling microhabitats for bryophytes, which we suspect to endure similar abiotic stresses at the ground level.

At each elevation level, therefore, a total of 108 samples of 50 cm² was achieved if all microhabitats were present and occupied by bryophytes, yielding a potential 648 samples for the transect. In the end, 296 samples of 50 cm² were collected and all bryophytes identified to species level (944 identifications). Bryophyte nomenclature and taxonomy follows Ah-Peng and Bardat (2005).

Species were categorized as elevational specialists or elevational generalists based on the total transect sampling and a geographic information system (GIS) database of La Réunion bryophytes (12,765 records). Specialists are those found only at or above 2150 m, while generalists have a wider elevational range on the island.

TRAIT DATA COLLECTION

Literature on functional traits for non-vascular plants is scarce and the functional significance of these traits is still poorly known (for a review, see Cornelissen et al., 2007). For the purpose of this study, we scored eight traits that are likely to be associated with resource utilization, or represent adaptations to the harsh conditions of the highlands: (1) stem length, (2) stem diameter, (3) presence or absence of secondary pigments, (4) presence/absence of a hyaline hair point at the apex of the leaf, (5) presence or absence



Subalpine and alpine habitats

FIGURE 1. Map of La Réunion Island with the subalpine shrubland vegetation highlighted. Sources: Fonds cartographiques — MNT IGN BD Topo Réunion 2003, and Habitats terrestres, UMR CIRAD, Université de La Réunion PVBMT. Authors: D. Strasberg, M. Rouget, D. M. Richardson, S. Baret, J. Dupont, and R. M. Cowling.

of lamellae, (6) presence or absence of papillae, (7) whether leaves are dissected or not, and (8) growth form.

Size and surface area-to-volume ratio are important for bryophytes as they affect the rate at which extracellular water is lost and at which they dry out. Here *stem length and diameter* were selected as size variables.

Secondary pigments are yellow- or orange-pigmented secondary metabolites. The functional significance of these compounds is not well understood, but they seem to play a role in anti-microbial protection, as well as protection from ultraviolet (UV) radiation (Xie and Lou, 2009).

Hyaline hair point refers to the hyaline apex of the elongated leaf blade, which for some species can be an extension of the costa. It is hypothesized that species having hyaline hair points can minimize water loss by controlling the orientation of their hair point (>90°) during dry periods, forming a thick boundary layer with quieter air, reducing the rate of water loss (Proctor, 2008). A hyaline hair point also prevents water loss by reflecting solar radiation (Zhang and Wang, 2008) and protecting leaves from sunburn (Zheng et al., 2009a, 2009b). A study from Tao and Zhang

(2012) recently confirmed that the presence of *hyaline hair points* increases the absorption of condensed water vapor from dew and water retention time. *Leaf surface papillae* appear to aid water uptake by creating capillary channels on the leaf surface. *Lamellae* are usually found in the abaxial or adaxial side of the leaf. They are formed of unistratose parallel photosynthetic cells arranged in rows and increasing the photosynthetic surface of the plant. Swelling of these lamellae (Van Zanten, 1974) provokes the movement of the wings of the leaf over them and results in the leaf being reflexed under moist conditions, and inflexed in dryer conditions, retarding water loss. In some Polytrichaceae species, the tips of lamellae also have a waxy covering that repels water, thus facilitating gas exchange (Proctor, 1979). By increasing more than six times the projected area of the leaf, lamellae increase CO₂ uptake in Polytrichaceae and provide a more efficient utilization of high irradiance of direct sunlight (Proctor, 2005). *Leaf dissection* refers to species that have divided pointed lobes, which could act similarly as hyaline hair points. Different *growth forms* of bryophyte gametophytes represent different strategies related to water conduction, retention, and gas exchange for pho-

tosynthesis: compact cushions or thick mats are most commonly found in well-drained habitats, as they are the slowest to dry out (Proctor, 1981), which enables the plant to stay wetter for longer. Isolated fan or dendroid growth forms are more commonly found in habitats where relative humidity is much higher as these forms dry out quickly. The cushion growth form could trap litter from its own production and/or blown away from surrounding plants, possibly contributing to nutrient enrichment but also promoting soil cohesion of the substrate.

These traits have been reported to play a role in water relations (e.g., Hedderson and Longton, 1995, 1996), resistance to desiccation, protection from UV and solar radiation, photosynthetic activity, and soil cohesion. We recorded these traits from the scattered taxonomic literature or, when the information was not available, by observation of herbarium specimens. It is important to note that most bryophyte traits used in literature are qualitative rather than quantitative, and that relationships with ecosystem functions have been poorly investigated. Measurements of stem lengths and diameters were done on six gametophytes and an average measurement was recorded in our data set.

Based on various literature sources, species were placed in the following distributional categories: African, disjunct America-Africa, paleotropical, pantropical, and subcosmopolitan. African species were divided into Afr3, which represents species restricted to Madagascar and neighboring islands, and End, which are species endemic to the Mascarenes.

DATA ANALYSIS

We compared bryophyte composition among the two communities and for every combination of studied elevations using the Bray-Curtis dissimilarity index (*BC*) based on presence-absence data, where *A* and *B* are the number of species at two different elevations and *J* is the number of species shared between the two.

$$BC = \frac{(A + B - 2 \times J)}{(A + B)} \quad (1)$$

Elevational bryophyte community similarities were grouped using average cluster analysis (Jongman et al., 1995).

Of the three independent multifaceted indices that describe the distribution of species and their abundance within functional space (Villéger et al., 2008; Laliberté and Legendre, 2012), two, *FEve* (Functional evenness) and *FDiv* (Functional divergence), describe the evenness of abundance distribution in functional trait space and how abundance is distributed within the volume of functional space. Since our analysis is based on presence-absence community matrices, we used the third index functional richness (*FRic*), which measures the functional space filled by a given species assemblage. The trait data set recorded eight traits (six binary and two continuous) for 99 species. Relationships between *FRic* and species richness and elevation were investigated using Pearson's rank coefficient of correlation. We explored univariate relationships between *FRic* and both species richness and elevation for each of the bryophyte communities. We tested for both linear and nonlinear relationships for each response measured and selected the best fit using the Akaike Information Criteria (Burnham and Anderson, 2004).

Data analyses were done using the statistical software R 2.15.1 (R Core Team, 2012) and the Vegan, Labdsv, and FD packages.

Results

SPECIES RICHNESS

In total, 99 bryophyte species were recorded in the 2150–3050 m interval. With 66 species, mosses were the most species-rich group, while 33 liverworts were present; no hornworts were recorded at these high elevations. Twenty-three families were recorded, with the moss family Dicranaceae (19% of species) exhibiting the greatest diversity, while Lejeuneaceae, with 10% of species, was the most diverse liverwort family. At the low end, 17 families altogether accounted for less than 5% of the total diversity.

Three families were restricted on the island to these subalpine shrublands—the moss families Andreaeaceae (*Andreaea* spp.) and Grimmiaceae (*Racomitrium* and *Grimmia* spp.) and the liverwort family Arnelliaceae (*Gongylanthus* spp.). Approximately 46% of the species were of African origin, with 19% endemic to the Afr3 region (Madagascar and neighboring islands). Of the latter, 10 are Mascarene endemics while only two are endemic to the island. Subcosmopolitan species made up 25% of the total, while pantropical, paleotropical, and disjunct America-Africa made up, respectively, 11%, 5%, and 3% of the flora.

The humicolous and corticolous habitats, with 9 and 8 species each, hosted the majority of the Mascarene endemics. The highest diversity of regional endemics (Afr3, Mascarene, or La Réunion) was recorded at 2150 and 2350 m in the lower subalpine habitats, at the limit with the forest system.

ELEVATIONAL VARIATION OF SUBALPINE BRYOPHYTE DIVERSITY WITHIN MICROHABITATS

Diversity showed a different relationship with elevation between the two communities (Fig. 2, encapsulated graph). The epiphytic species exhibited a hump-shaped diversity pattern, with a peak of diversity in the cloud forest around 1350 m a.s.l. (Ah-Peng et al., 2012). The ground-dwelling community (terricolous, humicolous, and rupicolous), showed a double peak of diversity, with the first in the cloud forest and a second at 2750 m. Above 2150 m (Fig. 2, main graph), which corresponds to the treeline, diversity in the corticolous microhabitat decreased with elevation concomitant with a decrease in substrate (tree/shrub trunks) availability. For the ground-dwelling community, the second peak observed comprised humicolous and rupicolous bryophytes, while the terricolous bryophyte community followed an opposite trend. The humicolous microhabitat was the most diverse within the ground-dwelling community. Cluster analysis shows that bryophyte communities of these uplands comprise three distinct groups: the community at the treeline (2150 m), the 2350–2750 m community, and the summit community (2950–3950 m).

Surprisingly, the diversity near the summit remains high (15 species), made up mostly of moss species. Liverwort richness decreases from treeline to the mountaintop, and from 2350 m to the highest elevation mosses dominate (Fig. 3, part a). As shown in Figure 3, part b, a high number of elevation-specialists (34% to 72% of total species) was present in the intermediate species assemblage (2350–2750 m), while at the limits of this gradient the flora largely comprised elevation-generalists.

The bryophyte assemblages of the ground-community were very similar along this transect, sharing 35% to 43% of their species richness. Ground- and trunk-dwelling bryophyte communities are quite distinct from each other, with 80% to 90% dissimilarity.

Eight different growth forms were present, with mat and erect forms accounting respectively for 25% and 19% of total species.

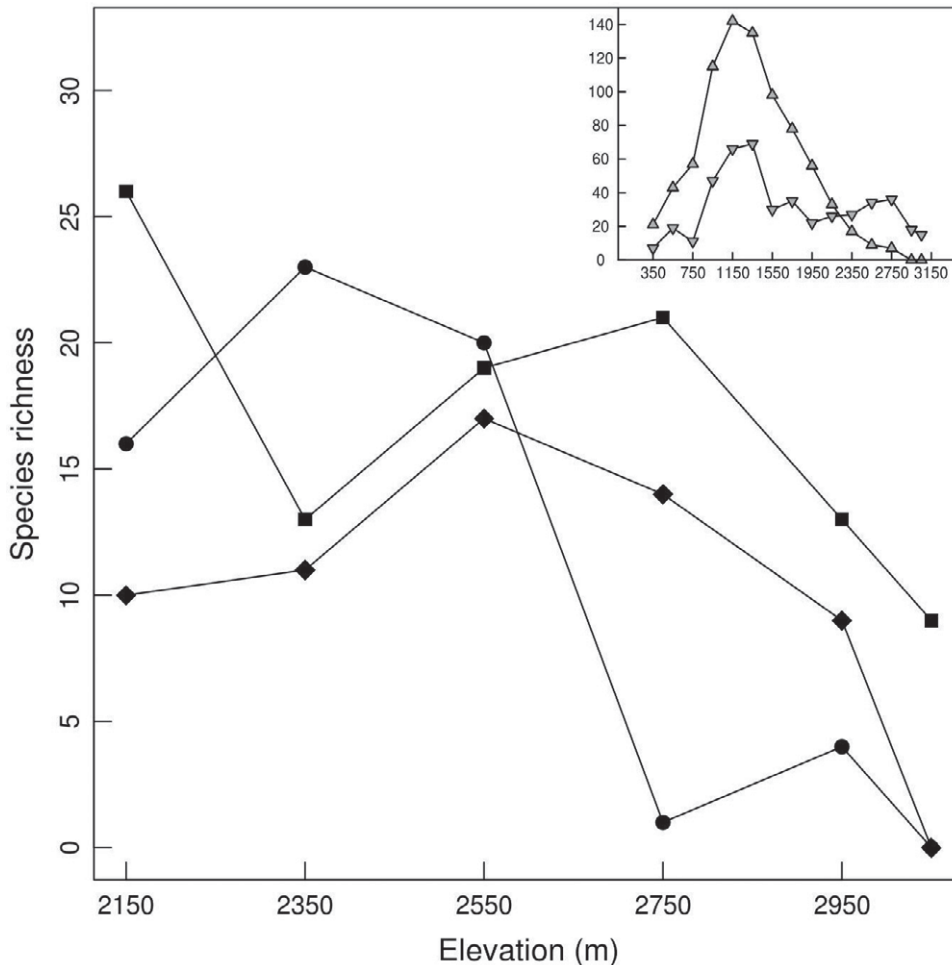


FIGURE 2. Diversity patterns for ground-dwelling bryophytes: terricolous (●), rupicolous (◆), and humicolous (■) along an elevational gradient (2150–3050 m a.s.l.). Upper top graph: diversity curves for epiphytic (Δ) and ground (▽) bryophyte communities from 350 to 3050 m.

The distribution of growth form differed between microhabitats, with erect mosses (e.g., *Campylopus* spp.) and liverwort mats (*Lethocolea* sp.) predominating in the humicolous microhabitat, while in corticolous and terricolous communities, the mat and tall turf growth forms, respectively, dominated. Erect above a fine organic matter layer (*Dicranella* sp., *Pohlia* sp., *Pleuridium* sp.), cushion (*Bryum argenteum*) and short turf (*Andreaea* spp.) were the growth forms most commonly found for rupicolous species.

In Figure 4, the eight growth forms are grouped into three main categories: erect short turfs or cushions, dense and tall turfs, and mats, fans, or wefts. From the treeline to the summit, the number of species exhibiting this last growth form decreased, suggesting that it is associated with more shaded and sheltered habitats. Most species at the highest elevations form erect short turfs and cushions, and these appeared to be the preferred growth forms in these open arid habitats.

FUNCTIONAL DIVERSITY

For both communities, functional richness (FRic) increased significantly with species richness with similar slopes (Fig. 5), but the correlation was much stronger ($r = 0.91, p < 0.001$) for the epiphytic than for the ground community ($r = 0.61, p < 0.001$). These positive linear relationships indicate low redundancy for both epiphytic and ground-dwelling communities. FRic decreased with elevation

in both communities, although with contrasting statistical support. For epiphytes, FRic showed a significant negative relationship with elevation (Spearman's $r = -0.71, p < 0.01$, hyperbolic model [AIC = -34.3] vs. linear [AIC = -32.5], $\Delta d.f. = 0$), suggesting higher functional diversity and limiting similarity at the treeline compared to lower functional diversity near the summit. For the ground-dwelling community, FRic marginally decreased with elevation (Spearman's $r = -0.36 < 0.1$) but with large variation at any given elevation, indicating that a wide variety of functional strategies coexist, and that communities are spatially heterogeneous.

Discussion

DIVERSITY PATTERN

With 99 species, dominated by mosses, these highland bryophyte communities are relatively species-rich and include nearly 12% of the total bryophyte diversity on the island. In comparison to vascular plants in the studied plots, 67% of which are strictly endemic, bryophytes show low levels of endemism. This is presumably because of their greater vagility, and ability to disperse over long distances by small wind-borne spores. This prevents complete genetic isolation in these sky island systems, in contrast with angiosperms where high peaks function as islands in a “sea of lowland” (Fernández-Palacios, this issue). The global distribution

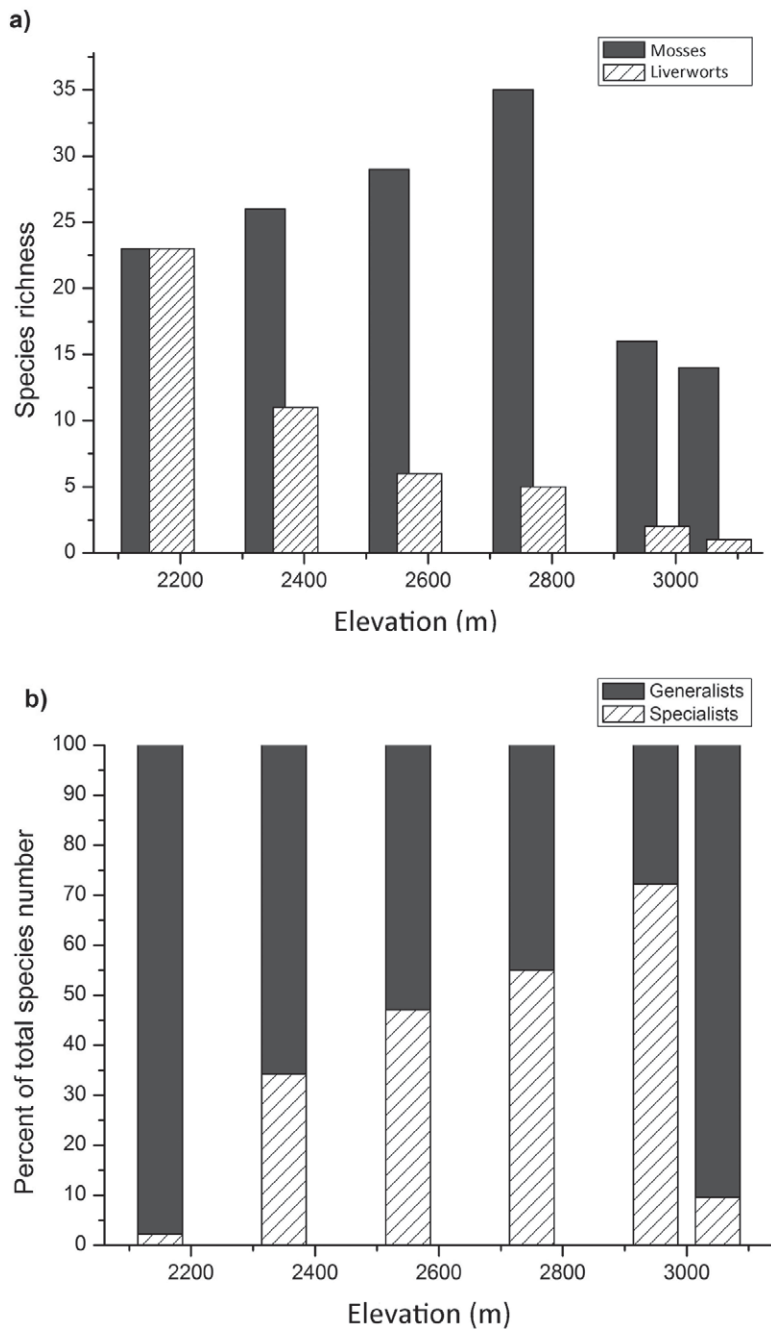


FIGURE 3. (a) Ratios of liverworts to mosses, and (b) specialists to generalists along the upper elevational gradient of Piton des Neiges volcano.

of this highland bryophyte flora suggests that half of the species are of African origin and almost 40% are from the Afr3 region, meaning that these species are part of a regional species pool and form specific assemblages in the Western Indian Ocean area.

While both bryophyte communities show a peak in species richness in the mountain cloud forest (Ah-Peng et al., 2012), in this paper we focus on the highest elevations and document a second peak of richness at 2750 m contributed mainly by the ground community. In these subalpine environments, the speciose humus microhabitat occurs among roots at the base of shrubs, or between rocks and soil, where organic matter and litter accumulate, providing nutrient-rich substrate with good moisture-holding capacity from which bryophytes may benefit (Rincon, 1988; Sun et al., 2013). A similar bimodal pattern of diversity has recently been

shown for terrestrial bryophytes in the Gongga Mountains in China, with a second peak of species richness above 3650 m a.s.l. (Sun et al., 2013). The development of the ground-dwelling bryophyte community at these high altitudes seems to fill empty niches, with almost no competition from vascular plants that show low cover and diversity here. The cluster analysis distinguished three groups along this transect: the treeline ecotone, the intermediate, and summit communities, with a peak of diversity in the intermediate community. Interestingly, this intermediate area also hosts a high number of elevationally restricted or specialist species (Fig. 3, part a), including the highest number of regionally endemic species. Similar results for endemic species were reported in Asia, where endemic species are usually less frequent in the summit floras but reach greatest abundance in the lower alpine zone (Agahanyanz

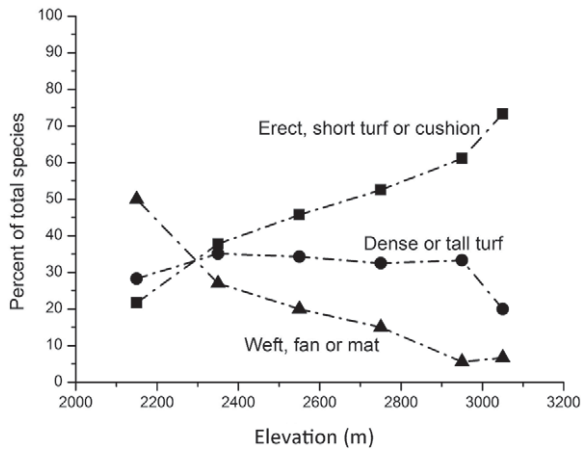


FIGURE 4. Bryophyte growth forms spectra (relative fraction of total reported bryoflora % per elevation) on subalpine habitats of Piton des Neiges volcano.

and Breckle, 1995). Mountaintops are commonly dominated by otherwise widespread species (Körner, 2003), and this view is supported in this study for the bryophyte communities.

These subalpine bryophyte communities exhibit a variety of growth forms on the Piton des Neiges, with most species being perennial. The dominance of species forming cushions or erect, short turves at high elevation can be related to water holding capacity. These growth forms, with high densities of gametophytes (e.g., cushions; Zotz et al., 2000), favor water retention by limiting water evaporation because of the smaller surface-to-volume ratio. These architectures are also believed to offer better protection against high UV radiation and low temperature.

In this study, we show that species richness of both bryophyte communities is positively correlated with functional richness. Similar patterns have been reported for tropical leaf litter ants in Brazilian forests (Bihn et al., 2010) and tadpole communities in Madagascar (Strauß et al., 2010). The relationship between FRic and S for the epiphytic assemblages is strong and shows no evidence of saturation, indicating low levels of redundancy among coexisting species. In other words, trunk-dwelling bryophytes tend to be functionally complementary, leading to local assemblages of functionally diverse and unique species. In contrast, FRic of the ground community showed some redundancy and evidence of stronger stochasticity, indicating that multiple species may perform similar functions (overlap of FRic).

Contrasting results for bryophyte ground- and trunk-dwelling communities indicate that different processes may act differently on the bryophyte communities, or that different bryophyte communities have different sensitivities to abiotic conditions according to their microhabitat. Ground bryophytes may have a greater tolerance of the extreme conditions and be better adapted to colonize these subalpine environments.

We demonstrate that FRic decreases with elevation in these subalpine communities, presumably associated with increasing harshness (open, xeric environments). For the corticolous community, this is probably due to the drastic change in species richness and diversity of assemblages from 2150 m (mesic forest, cool and moist) to 2950 m (subalpine shrubland systems, arid and dry). This loss of functional diversity at the quadrat level can also be directly related to a decrease in species richness for the corticolous microhabitat. The higher functional richness at lower elevations (near treeline) is in accordance with theory, which suggests that competition may be the main assembly rule in species-rich systems. It is also compatible with a physiological tolerance hypothesis, which

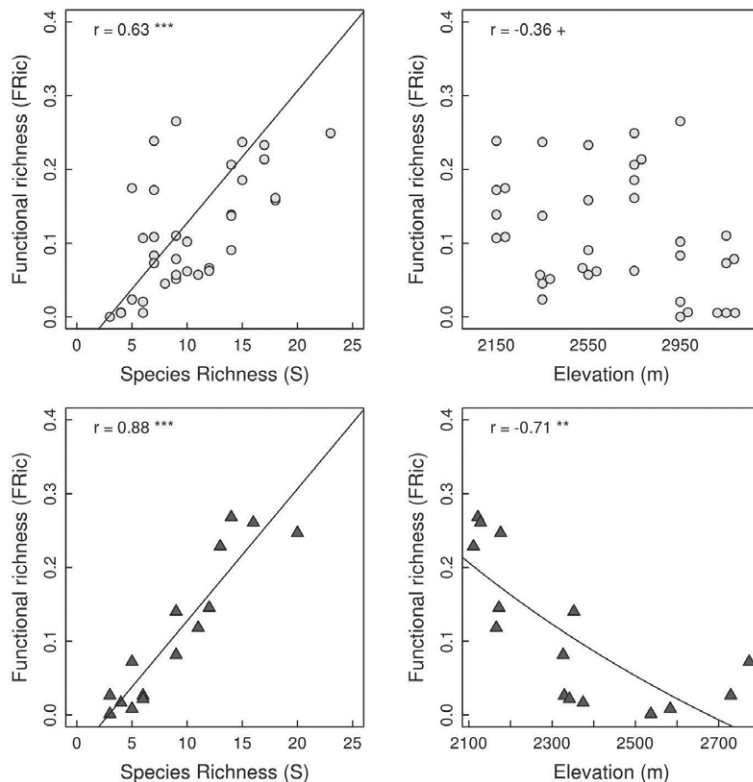


FIGURE 5. Scatter plots of species richness and elevation against functional richness (FRic) on the upslope of the Piton des Neiges volcano for ground (circles) and epiphytic communities (triangles). Pearson rank's correlation is significant (*: $p < 0.001$, **: $p < 0.01$, +: $p < 0.1$). Marginal trend in FRic against elevation for ground-dwelling communities.**

postulates that benign climates support higher species richness by permitting a wider variety of plant functional strategies to coexist (Currie et al., 2004; Spasojevic et al., 2014).

Stochasticity in the response of FRic to elevation in this community may be closely linked to the fact that ground-dwelling species share traits. This implies that loss of species may not greatly affect FRic, and that environmental filtering could be the main force structuring this rich community. We cannot exclude the possibility that adding more traits would increase our ability to detect functional differences along the elevational gradient. In addition, the fact that six of the eight studied traits are binary might also artificially inflate levels of functional redundancy.

Facilitation (positive interactions) has largely been neglected in ecological theories, which are mostly based on negative interactions (predation, competition). Facilitation could play an important role in the assembly of bryophyte communities and better explain species-rich systems than competition and environmental filtering. In the species-rich corticolous assemblages, for example, tiny liverworts often occur within moss cushions, possibly benefiting from favorable conditions (i.e., higher humidity and substrate). It is difficult to disentangle the different mechanisms involved in the assembly of bryophyte communities, as the performance of cryptogam species is frequently positively density-dependent, and intraspecific facilitation is suspected to be the norm rather than the exception (Cornelissen et al., 2007).

Incorporation of such effects is clearly essential for increasing our understanding of assembly rules in these systems. Coupling functional diversity approaches with phylogenetic information is another necessary step that will allow us to account for the effect of species relatedness in structuring diversity. It is clear that, in general, cryptogams may not follow the same assembly rules as vascular plants.

Bryophytes are fundamentally different from vascular plants and offer a unique system for testing ecological theories and elucidating the mechanisms behind biodiversity and ecosystem functions.

CONSERVATION OF SUBALPINE BRYOPHYTE COMMUNITIES AND HABITATS IN LA RÉUNION

This study shows that bryophytes represent an important diversity and functional component in the subalpine ecosystems of the Piton des Neiges. The relatively species-rich intermediate system between the treeline and mountaintop (the peak of richness in ground-dwelling bryophytes at 2750 m) has accumulated the highest number of elevationally restricted species, many also having restricted global distributions including regional endemics. These systems thus require a greater degree of attention because these organisms have nowhere to escape to should these habitats come under threat (shift of treeline upward at the expense of alpine communities and habitat destruction).

This preliminary work on the structure of functional diversity in these subalpine environments showed high levels of redundancy in the ground-dwelling subalpine communities, indicating on one hand that they may be more resilient to disturbances than epiphytic bryophytes but, on the other hand, as species richness is low at the mountaintop (15 mosses), a loss of species would affect greatly the functions of ecosystems.

Provision of baseline data for bryophyte richness and distribution, and inclusion of these lesser studied plants into “mountain watch” programs, would be timely as they can also serve as sensitive, early indicators of change.

Acknowledgments

The authors would like to thank the National Park of Réunion for the collecting permit (no. 2008/1020/BL) and also the organizing committee of the Tropical Alpine and Subalpine Conference in Hawaii, for covering expenses of Ah-Peng to attend this meeting. We thank Hashradah Ramburn for collecting some of the trait data for this study. We are grateful to the Claude Leon Harris Foundation for the postdoctoral fellowship of Ah-Peng. This manuscript was finalized while Ah-Peng and Wilding were visiting Bernard Goffinet’s laboratory at the Ecology and Evolutionary Biology department at the University of Connecticut supported by the University of Cape Town travel grants. Logistic support was provided by the field station of Mare Longue (P.O.E Réunion 2.02 and OSU Réunion). This work was realized in the framework of the research program MOVECLIM and benefited from the support of the Agence Nationale de la Recherche, Conseil régional de La Réunion, Conseil régional de Guadeloupe, Government of Azores, Government of Canarias, under the framework of Net-Biome transnational first call.

References Cited

- Agahanyanz, O. E., and Breckle, S. W., 1995: Origin and evolution of the montane flora of middle Asia and neighbouring mountain regions. In Chapin, F. S. I., and Körner, C. (eds.), *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystems Consequences*. Berlin: Springer Verlag, 63–80.
- Ah-Peng, C., and Bardat, J., 2005: Check list of the bryophytes of Réunion Island (France). *Tropical Bryology*, 26: 89–118.
- Ah-Peng, C., Chuah-Petiot, M., Descamps-Julien, B., Bardat, J., Staménoff, P., and Strasberg, D., 2007: Bryophyte diversity and distribution along an elevational gradient on a lava flow in La Réunion. *Diversity & Distribution*, 13: 654–662.
- Ah-Peng, C., Bardat, J., Ellis, L., Hedderson, T. A. J., Malombe, I., Matcham, H., Pöcs, T., Porley, R., Séneca, A., Söderstrom, L., and Wilbraham, J., 2010: Additions to the bryoflora of Réunion Island 3: new and interesting records from the Tropical Bryology Group (British Bryological Society). *Journal of Bryology*, 32: 288–295.
- Ah-Peng, C., Wilding, N., Kluge, J., Descamps-Julien, B., Bardat, J., Chuah-Petiot, M., Strasberg, D., and Hedderson, T., 2012: Bryophyte diversity and range size distribution along two elevational gradients: continent vs. island. *Acta Oecologica*, 42: 58–65.
- Barcelo, A., 1996: Analyse des mécanismes hydrologiques sur domaine volcanique insulaire tropical à relief jeune. Apports à la connaissance du bilan hydrique. Massif du Piton de la Fournaise (île de la Réunion). Ph.D. thesis, Montpellier II, Montpellier.
- Bihn, J., Gebauer, G., and Brandl, R., 2010: Loss of functional diversity of ant assemblages in secondary tropical forest. *Ecology*, 91: 782–792.
- Burnham, K. P., and Anderson, D. R., 2004: Multimodel inference—Understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33: 261–304.
- Caujapé-Castells, J., Tye, A., Crawford, D. J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, V. F. B., Moura, M., Jardim, R., Gúmes, I., and Kueffer, C., 2010: Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 12: 107–129.
- Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C., and Longino, J. T., 2008: Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322: 258–261.
- Corlett, R. T., 2012: Climate change in the tropics: the end of the world as we know it? *Biological Conservation*, 151: 22–25.
- Cornelissen, J. H. C., Lang, S. I., Soudzilovskaia, N. A., and During, H. J., 2007: Comparative cryptogam ecology: a review of bryophytes and lichen traits that drive biogeochemistry. *Annals of Botany*, 99: 987–1001.

- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J. F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, R., and Turner, J. R. G., 2004: Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7: 1121–1134.
- De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R. D., Berg, M. P., Cipriotti, P., Feld, C. K., Hering, D., Martins da Silva, P., Potts, S. G., Sandin, L., Sousa, J. P., Storkey, J., Wardle, D. A., and Harrison, P. A., 2010: Towards an assessment of multiple ecosystem processes and services *via* functional traits. *Biodiversity and Conservation*, 19: 2873–2893.
- Hardin, G., 1960: Competitive exclusion principle. *Science*, 131: 1292–1297.
- Hedderson, T. A. J., and Longton, R., 1995: Patterns of life history variation in the Funariales, polytrichales and Pottiales. *Journal of Bryology*, 18: 639–675.
- Hedderson, T. A. J., and Longton, R., 1996: Life history variation in mosses, water relations, size and phylogeny. *Oikos*, 77: 31–43.
- Jongman, R. H. G., ter Braak, C. J. F., and Van Tongeren, O. F. R., 1995: *Data Analysis in Community and Landscape Ecology*. Cambridge: Cambridge University Press.
- Körner, C., 2003: *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Heidelberg: Springer Verlag, 344 pp.
- Lacoste, M., and Picot, F., 2011: *Cahiers d'habitats de La Réunion: étage altimontain. Rapport technique n° 7 non publié*. Saint-Leu, Réunion: Conservatoire Botanique National de Mascarin.
- Laliberté, E., and Legendre, P., 2012: A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91: 299–305.
- Li, Y., and Qi, Z., 1993: Primary production of alpine-shrub-moss type grassland in Qilian Mountains and responses of soil ecosystems to disturbances. *Acta Prataculturae Sinica*, 2: 66–74.
- MacArthur, R. H., and Levins, R., 1967: Limiting similarity convergence and divergence of coexisting species. *American Naturalist*, 101: 377–385.
- Micheli, F., and Halpern, B. S., 2005: Low functional redundancy in coastal marine assemblages. *Ecology Letters*, 8: 391–400.
- Mouchet, M., Villéger, S., Mason, N. W. H., and Mouillot, D., 2010: Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24: 867–876.
- Mouillot, D., Dumay, O., and Tomasini, J. E., 2007: Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine, Coastal and Shelf Science*, 71: 443–456.
- Naeem, S., 2002: Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. *Ecology*, 83: 2925–2935.
- Poos, L. S., Walker, S. C., and Jackson, D. A., 2009: Functional-diversity indices can be driven by methodological choices and species richness. *Ecology*, 90: 341–347.
- Proctor, M. C. F., 1979: Structure and eco-physiological adaptations in bryophytes. In Duckett, J. G., and Clarke, G. C. S. (ed.), *Bryophyte Systematics*. London: Systematics Association Special Volume, 479–509.
- Proctor, M. C. F., 1981: Diffusion resistance in bryophytes. In Grace, J. (ed.), *Plants and their atmospheric environment. 21st Symposium of the British Ecological Society*. Oxford: Blackwell Scientific Publications, 219–229.
- Proctor, M. C. F., 2005: Why do Polytrichaceae have lamellae? *Journal of Bryology*, 27: 221–229.
- Proctor, M. C. F., 2008: Physiological ecology. In Goffinet, B., and Shaw, J. (eds.), *Bryophyte Biology*, 2nd edition. Cambridge: 237–268.
- R Core Team, 2012: R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rincon, E., 1988: The effect of herbaceous litter on bryophyte growth. *Journal of Bryology*, 15: 209–217.
- Robinson, S. A., and Waterman, M. J., 2014: Sunsafe bryophytes: photoprotection from excess and damaging solar radiation. In Hanson, D. T., and Rice, S. K. (ed.), *Photosynthesis in Bryophytes and Early Land Plants. Advances in Photosynthesis and Respiration*, volume 37. Dordrecht, Netherlands: Springer, 113–130.
- Spasojevic, M. J., Grace, J. B., Harrison, S., and Damschen, E. I., 2014: Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradient. *Journal of Ecology*, 102: 447–455.
- Stevens, R. D., Cox, S. B., Strauss, R. E., and Willig, M. R., 2003: Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters*, 6: 1099–1108.
- Strasberg, D., Rouget, M., Richardson, D. M., Baret, S., Dupont, J., and Cowling, R. M., 2005: An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. *Biodiversity and Conservation*, 14: 3015–3032.
- Strauß, A., Reeve, E., Randrianiaina, R.-D., Vences, M., and Glos, J., 2010: The world's richest tadpole communities show functional redundancy and low functional diversity: ecological data on Madagascar's stream-dwelling amphibian larvae. *BMC Ecology*, 10: 1–10.
- Sun, S.-Q., Wu, Y.-H., Wang, G.-X., Zhou, J., Yu, D., Bing, H.-J., and Luo, J., 2013: Bryophyte species richness and composition along an altitudinal gradient in Gongga Mountain, China. *PLoS One*, 8 (3): e58131.
- Tao, Y., and Zhang, Y. M., 2012: Effects of leaf hair points of a desert moss on water retention and dew formation: implications for desiccation tolerance. *Journal of Plant Research*, 125: 351–360.
- Theurillat, J.-P., Schlüssel, A., Geissler, P., Guisan, A., Velluti, C., and Wiget, L., 2003: Vascular plants and bryophyte diversity along elevational gradients in the Alps. In Nagy, L., Grabherr, C., Körner, Ch., Thompson, D. B. A. (eds.), *Alpine Biodiversity in Europe. Ecological Studies*, volume 167. Berlin: Springer, 185–193.
- Van Zanten, B. O., 1974: The hygroscopic movement of the leaves of *Dawsonia* and some other Polytrichaceae. *Bulletin de la Société Botanique de France*, 121: 63.
- Villéger, S., Mason, N. W. H., and Mouillot, D., 2008: New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89: 2290–2301.
- Weiherr, D. J., and Keddy, P. A., 1995: Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74: 159–164.
- Xie, C.-F., and Lou, H.-X., 2009: Secondary metabolites in bryophytes: an ecological aspect. *Chemistry and Biodiversity*, 6: 303–312.
- Zhang, Y. M., and Wang, X. Q., 2008: *Study on the Microbiotic Crusts in Junggar Desert*. Beijing: Science Press, 155 p.
- Zheng, Y. P., Zhao, J. C., Zhang, B. C., Li, L., and Zhang, Y. M., 2009a: Advances on ecological studies of algae and mosses in biological soil crust. *Chinese Bulletin of Botany*, 44: 371–378.
- Zheng, Y. P., Zhao, J. C., Zhang, B. C., and Zhang, Y. M., 2009b: Morphological and structural adaptation and characteristics of protonemal development of *Syntrichia caninervis* in the mosses crust layer. *Journal of Desert Research*, 29: 878–884.
- Zobel, M., 1997: The relative role of species pool in determining plant species richness. An alternative explanation of species coexistence? *Trends in Ecology and Evolution*, 12: 266–269.
- Zotz, G., Schweikert, A., Jetz, W., and Westerman, H., 2000: Water relations and carbon gain in relation to cushion size in the moss *Grimmia pulvinata* (Hedw.) Sm. *New Phytologist*, 148: 59–67.

MS accepted May 2014

APPENDIX

TABLE A1

Data set of 8 traits for 99 bryophyte species: growth form, stem length and stem diameter, presence/absence of secondary pigments, hyaline hairpoint, papillae, lamellae, and dissected leaves.

Species	Abbreviation	sec_pig	hya_hair	papillae	growth_form	lamellae	diss_leaves	stem_length	stem_diam
<i>Anastrophyllum piligerum</i> (Nees) Steph.	anas_pili	1	1	0	m	0	1	11	0.2
<i>Bazzania mascarena</i> (Steph.) Herzog	bazz_masc	0	0	0	w	0	0	15	0.41
<i>Campylopus arctocarpus</i> ssp. <i>madecassus</i> (Besch.) J.-P. Frahm	camp_arct	1	0	0	tt	1	0	30	0.19
<i>Campylopus aureonitens</i> (Müll.Hal.) A. Jaeger	camp_aure	1	0	0	e	1	0	8	0.18
<i>Campylopus crateris</i> Besch.	camp_crat	1	1	0	e	0	0	45	0.233
<i>Campylopus flexuosus</i> (Hedw.) Brid.	camp_flex	1	1	0	tt	0	0	17.5	0.15
<i>Campylopus robillardiei</i> Besch.	camp_robi	1	0	0	tt	0	0	NA	NA
<i>Campylopus</i> sp. 1	camp_sp1	1	0	0	tt	0	0	NA	NA
<i>Cephaloziella kiaeri</i> (Austin) S.W. Arnell	ceph_kiar	1	0	1	m	0	1	6.5	0.09
<i>Cheilolejeunea surrepens</i> (Mitt.) E.W. Jones	chei_surr	0	0	0	m	0	0	30	0.07
<i>Cheilolejeunea usambarana</i> (Steph.) Grolle	chei_usam	1	0	0	m	0	0	35	0.095
<i>Dicranoloma billardierei</i> (Brid. ex Anon.) Paris	dicr_bill	1	0	0	e	0	0	65	0.318
<i>Diplasiolejeunea cornuta</i> Steph.	dipl_corn	1	0	0	m	0	0	15	0.06
<i>Drepanolejeunea physaeifolia</i> (Gottsche) Steph.	drep_phys	1	0	0	m	0	0	5.5	0.045
<i>Frullania apiculata</i> (Reinw.) Blume & Nees)	frul_apic	1	0	0	m	0	1	37.5	0.135
<i>Frullania borbonica</i> Lindenb.	frul_borb	1	0	0	m	0	0	15	0.1
<i>Frullania lindenbergii</i> Lehm.	frul_lind	1	0	0	m	0	0	25	0.19
<i>Herbertus dicranus</i> (Taylor ex Gottsche et al.) Trevis.	herb_dicr	1	1	1	e	0	1	70	0.24
<i>Holomitrium borbonicum</i> Besch.	holo_borb	1	0	0	dt	0	0	11	0.1
<i>Hypnum cupressiforme</i> Hedw.	hypn_cupr	0	0	0	m	0	0	35	0.255
<i>Solenostoma onraedtii</i> (Vàrà) Vàmà et al.	sole_onra	1	0	0	st	0	0	10	0.25
<i>Jungermannia</i> sp. 1	jung_sp1	1	0	0	st	0	0	NA	NA
<i>Leptodontium flexifolium</i> (With.) Hampe in Lindb.	lept_flex	1	0	1	tt	0	0	23.53	0.2
<i>Leucolejeunea xanthocarpa</i> (Lehm. et Lindenb.) A.Evans	leuc_xant	0	0	0	m	0	0	1.4	0.125

TABLE A1

Continued

Species	Abbreviation	sec_pig	hya_hair	papillae	growth_form	lamellae	diss_leaves	stem_length	stem_diam
<i>Macrocoma tenuis</i> (Hook. & Grev.) Vitt	macr_tenu	1	0	0	e	0	0	14.28	0.357
<i>Macrohymenium acidodon</i> (Mont.) Dozy & Molk.	macr_acio	0	1	0	m	0	0	21.42	0.142
<i>Macromitrium microstomum</i> (Hook. & Grev.) Schwägr.	macr_micr	1	1	0	c	1	0	35	0.12
<i>Macromitrium pallidum</i> (P.Beauv.) Wijk & Margad.	macr_pall	1	0	1	dt	0	0	23	0.2
<i>Microlejeunea africana</i> Steph.	micr_afri	0	0	0	m	0	0	0.23	0.0375
<i>Microlejeunea strasbergii</i> Bardat & Ah-Peng	micr_stra	0	0	0	m	0	0	1.75	0.175
<i>Plagiochila pectinata</i> Willd. ex Lindenb.	plag_pect	1	0	0	f	0	1	75	0.375
<i>Plagiochila renauldii</i> Steph.	plag_rena	1	0	0	f	0	0	30	0.375
<i>Plagiochila</i> sp. 1	plag_sp1	1	0	0	f	0	0	NA	NA
<i>Polytrichum commune</i> Hedw.	poly_comm	1	1	0	e	1	0	47	0.588
<i>Bucklandiella membranaceum</i> (Mitt.) Paris	buck_memb	1	1	0	tt	0	0	16.07	0.255
<i>Radula tabularis</i> Steph.	radu_tabu	1	0	0	m	0	0	20	0.12
<i>Rhaphidorrhynchium crispans</i> (Besch.) Broth.	rhap_cris	0	0	0	dt	0	0	NA	NA
<i>Schlotheimia angulosa</i> P.Beauv.	schl_angu	1	1	0	dt	0	0	NA	NA
<i>Schlotheimia badiella</i> Besch.	schl_badi	1	0	1	dt	0	0	22	0.19
<i>Ulota fulva</i> Brid.	ulot_fulv	1	0	0	c	0	0	6	0.17
<i>Zygodon reinwardtii</i> (Hornsch.) A. Braun	zygo_rein	1	0	1	e	0	0	19	0.142
	Presence:0								
	Absence:1								

Notes: fan (f), mat (m), weft (w), tall turf (tt), dense turf (dt), short turf (st), cushion (c), stem length and diameter in millimeters