




Scaling α - and β -diversity: bryophytes along an elevational gradient on a subtropical oceanic Island (La Palma, Canary Islands)

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Nomenclature

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Introduction

The striking ecological changes occurring along elevational gradients have attracted the attention of researchers over

Abstract

Questions: We addressed three questions: (1) what is the variation of α - and β -diversity of bryophyte communities across spatial scales in an elevational gradient; (2) is spatial variation characteristic of different phylogenetic (mosses/liverworts) and/or ecological groups (terrestrials/epiphytes); and (3) what is the contribution of species richness and species replacement (*true turnover*) to β -diversity along the elevational gradient?

Location: La Palma, Canary Islands, Spain.

Methods: An elevational transect spanning 0–2200 m a.s.l. was sampled at altitudinal intervals of ca. 200 m, two 10 m × 10 m plots were established at each elevation and inside each plot three 2 m × 2 m quadrats were randomly selected. Within each quadrat, bryophytes were sampled in three replicate microplots of 10 cm × 5 cm, for each substrate: soil, rocks, leaves, humus, decaying wood and tree trunks at three heights. We evaluated α - and β -diversity at plot and elevational level for all bryophytes and for phylogenetic and ecological groups. Values of β -diversity were further decomposed into replacement and richness differences. We tested the relationship between α - and β -diversity and elevation using linear models with and without a quadratic term (elevation²) in an AICc-based framework.

Results: A total of 121 species were recorded along the transect. Alpha-diversity showed a hump-shaped pattern with elevation for all bryophytes, liverworts and epiphytic species, however, terrestrial species and mosses displayed no clear pattern. Species replacement was the main driver of β -diversity for all bryophytes and also for mosses and terrestrial species, and at different scales (elevational belt and quadrat). The contribution of species replacement increased with elevation, except for epiphytes and terrestrials.

Conclusions: Our study contributes towards an understanding of the spatial organization of bryophyte diversity at different scales along an insular elevational gradient. We showed that bryophyte diversity was mostly influenced by species replacement at the largest scale. The observed differences in β -diversity decomposition between bryophyte phylogenetic and ecological groups could be dependent on climatic conditions and substrate availability. The strong differences observed along the elevational gradient related to *true turnover* are especially important in the current global change scenario.

recent centuries (Lieberman et al. 1996; Brown 2001; Lomolino 2001). Authors such as Darwin, Wallace and von Humboldt provided the first detailed observations of how natural communities change with elevation

(Lomolino 2001). The abiotic elevational gradient occurring on mountains is a key feature controlling species richness, abundance and distribution, and understanding how species assemble along elevational gradients is essential to promote long-term conservation of species and natural communities. Due to changes in composition and diversity of animals and plants with elevation and their associated abiotic factors, elevational gradients became a central topic in studies of ecology and evolution (Körner 2007). For decades, the decrease in species richness with increasing elevation was accepted as a general pattern in ecology, since the elevational gradient was widely claimed to mirror the latitudinal gradient (Rahbek & Museum 1995). However, further studies on different mountain systems have revealed that elevational patterns in species richness are more diverse (McCain 2009; McCain & Grytnes 2010; Sun et al. 2013).

Until recently, most studies of the species richness–elevation gradient implicitly assumed that the mechanisms generating elevational species richness patterns were similar at arbitrarily defined scales of analysis (Rahbek 2005). However, over the last decade, ecologists and conservation biologists have increased their focus on how diversity patterns vary across spatial scales. For instance, species co-occurrences are determined not only by the biotic and abiotic factors operating at the scale a group of organisms co-exist, but also by large-scale spatial and temporal forces such as historic and geographic forces that determine the species richness of that group (Böhning-Gaese 1997). Therefore, one important step in our understanding of elevational species richness patterns might be to emphasize the spatial scale or plot/quadrat size at which species richness is calculated (Wiens 1989).

Whittaker (1960) first acknowledged the link between diversity and spatial scale, and distinguished three main types of ‘inventory diversities’: local, ‘richness in species of a particular stand or community’ usually within-habitat (α); regional, ‘species diversity of a number of community samples’ at landscape scale (γ) and a measure of local vs regional diversity, ‘extent of change of community composition’ (β). Within-habitat α -diversity measures the species diversity of a homogeneous community, γ -diversity measures the species diversity of a landscape ‘including more than one kind of community’ and β -diversity measures the spatial or temporal variation of species diversity.

Several authors have recently proposed to further decompose β -diversity in different components, reflecting different ecological processes, such as nestedness, species turnover or replacement (Baselga 2010; Podani & Schmera 2011; Legendre 2014). Among them, Carvalho et al. (2012) have suggested distinguishing between (1) species replacement (turnover; substitution of species among sites) and (2) species richness differences (gain or loss of species

among sites; Podani & Schmera 2011; Carvalho et al. 2012, 2013). According to this perspective, in order to better interpret β -diversity patterns along elevation gradients, it seems necessary to disentangle the contribution of both sources of variation (Podani & Schmera 2011; Carvalho et al. 2012, 2013; Legendre 2014).

Most studies on the diversity and distribution of plants along elevational gradients have been performed using vascular plants as the representative organism. Comparatively, few descriptive studies of bryophytes and their elevational distributions have been carried out; some were performed in different islands such as La Réunion (Ah-Peng et al. 2007), Terceira, (Azores) (Henriques et al. 2016) and Borneo (Frahm 1990) and others in continental settings (van Reenen & Gradstein 1983; Sun et al. 2013). Bryophytes have been compared with other groups such as lichens, ferns, vascular plants (Kessler 2000; Grytnes et al. 2006; Grau et al. 2007) and even animals (Andrew et al. 2003).

However, to our knowledge, studies assessing patterns of bryophyte species richness along elevational gradients at different spatial scales are very scarce (but see Andrew et al. 2003), and no study assesses the contribution of the processes of replacement or species richness difference to total β -diversity along the gradient. Therefore, the aims of this study are three-fold: (1) to evaluate the patterns of α - and β -diversities at different spatial scales along an elevational gradient, (2) to quantify the contribution of species richness difference and replacement to β -diversity patterns across different spatial scales, and (3) to investigate whether those patterns differ between different phylogenetic (mosses and liverworts) and ecological groups (terrestrials and epiphytes).

Method

Study area

The archipelago of the Canary Islands, together with Madeira, belongs to the Canary-Madeiran Subregion of the Mediterranean biogeographical region (Rivas-Martínez 2007), which is part of one of the most remarkable biodiversity hotspots on the planet, the Mediterranean Basin (Médail & Quézel 1997; Myers et al. 2000), hosting an important percentage of endemism of both fauna and flora, well known for their richness of seed plants as well as for bryophytes. Bryophytes comprise some of the earliest land plants, currently classified in three evolutionary phyla (Bryophyta, Marchantiophyta and Anthocerotophyta), forming the second most diverse plant group, with more than 18 000 species (Mishler 2001; Crandall-Stotler et al. 2009; Goffinet et al. 2009; Renzaglia et al. 2009). Their world distribution ranges from the tropics to the Polar regions and from sea level to mountain summits, making

them ideal candidates for latitudinal and elevational studies (Andrew et al. 2003). The Canary Islands host a total of 503 bryophyte species (356 mosses, 141 liverworts and six hornworts; Losada-Lima et al. 2010), and more than two-thirds of these species ($N = 344$; 68.4%) are present in the island of La Palma (244 mosses, 94 liverworts and all hornworts), occupying an ecologically relevant elevational gradient.

The study was conducted in La Palma Island, which is one of the youngest islands of the archipelago, with an age of 1.6 Ma. It has a relatively small area (706 km²) but is the second highest island (2396 m a.s.l.; Roque de los Muchachos), encompassing the majority of ecosystems present in the Canary Islands. There are also a large variety of bioclimatic belts, particularly on the north and east slopes of the island. Below 1500 m a.s.l., these slopes are exposed to trade winds, which make them extremely humid. In La Palma, it is possible to recognize four main types of habitat. The lowland areas (0–200 m a.s.l.) are occupied by shrubby vegetation, dominated by species of the genus *Euphorbia*, which are adapted to the infra-thermomediterranean arid/semi-arid climate. Above the shrubland (200–400 m a.s.l.), the potential vegetation is a thermophyllous laurel forest, nowadays a highly fragmented habitat due to human influence. The potential area for the wetter laurel forest is located from 400 to 1400 m a.s.l. This vegetation type has been systematically destroyed in the island and only a few small patches of mature and well-preserved forest are still present. From

1500 to 2000 m a.s.l. there is an endemic pine (*Pinus canariensis*) forest. In the intermediate elevations, between 1200 and 1500 m a.s.l., a transition vegetation called mixed-pine forest is present, with elements of both laurel forest and pine forest. Above 1500 m fire is the most important factor of disturbance. Above the timberline (2000 m a.s.l.) the vegetation is dominated by the shrub *Adenocarpus foliolosus* included in the supra-mediterranean dry belt. Further descriptions of the habitats may be seen in Del Arco-Aguilar et al. (2006). The study area consists of an elevational transect, located on the northeast slope of the island, in an area where it was possible to find well-preserved native vegetation. Plots were established following two ravines; Barranco de La Galga and Barranco de Los Tilos, with the upper plot at 2200 m a.s.l. at Pico de Las Nieves (Fig. 1).

Sampling design

The fieldwork was conducted from Apr 2012 to Apr 2013. The sampling design followed the BRYOLAT methodology (Ah-Peng et al. 2012, 2014; Gabriel et al. 2014). We used a hierarchically nested design to sample bryophytes along an elevational gradient. Four hierarchical levels were represented in this design: elevational belts (stations), plots, quadrats and substrates (see Fig. 1). The gradient went from the coast (ca. 40 m a.s.l.) to the summit (ca. 2200 m a.s.l.). Within this transect, sampling sites were established approximately every 200 m (± 50 m if necessary), thus

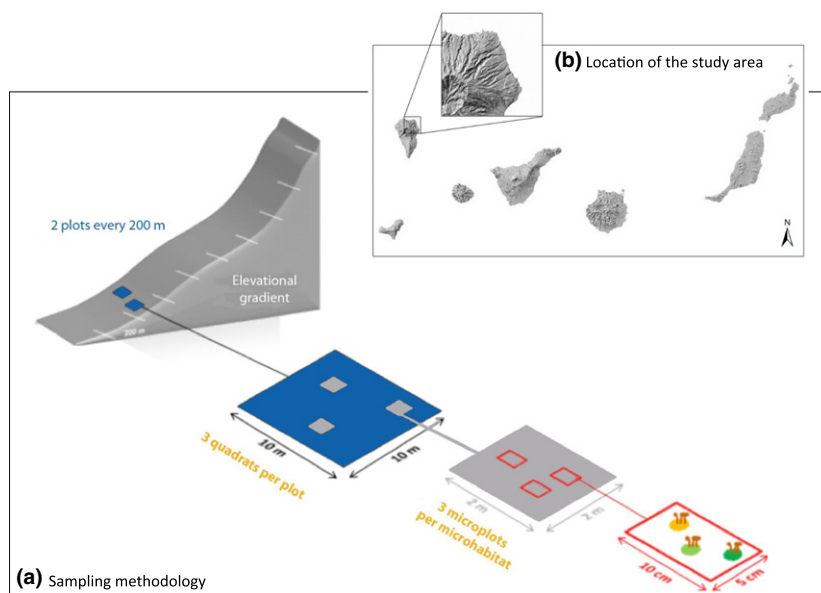


Fig. 1. (a) Representation of the sampling BRYOLAT methodology (transect on the island; at 200-m elevation steps, two plots (blue squares, 10 m x 10 m) are placed within 10–15 m of each other; each plot is divided into 25 quadrats from which three are sampled (grey squares, 2 m x 2 m); each quadrat is thoroughly examined for different substrata, and three microplots (red rectangular shapes, 5 cm x 10 cm) are collected on every microhabitat, except on trees, where nine replicates are made. (b) Location of the study site in La Palma Island (Canary Islands).

resulting in 12 elevational levels. Two plots were nested within each elevational level. The area of each plot was 10 m x 10 m, and within each area, detailed sampling of the vegetation was made, recording every vascular species present and their relative cover. Within each plot we randomly selected three 2 m x 2 m quadrats. Finally, in each quadrat, bryophytes were sampled from every present substrate (soil, rocks, living leaves, humus, decaying wood and tree trunks) in 10 cm x 5 cm samples (microplots). Generally, three replicates were collected of each substrate within each quadrat but epiphytic bryophytes were collected on three trees, at three different heights (TA: 0–50 cm, TB: 50–100 cm; TC: 100–200 cm). Usually, bryophyte samples were first identified in the field, to estimate cover, and then taken to the lab for confirmation. All samples are deposited in the herbarium TFC-Bry of La Laguna University.

Alpha- (α) and β -diversity measurement

In the following analyses, we used presence–absence data and we considered two scales of analysis: elevation belt (all species found across microplots within a belt) and quadrats (all species found across microplots within a quadrat). All the following analyses were performed separately for the subsequent groups: (1) all bryophyte species; (2) liverworts; (3) mosses; (4) all terrestrial species (including bryophytes growing on humus, soil and rock); and (5) epiphyte species (bryophytes growing on living bark and on decaying wood. No bryophyte was observed growing on leaves).

We defined α -diversity at two distinct spatial scales: we first calculated the α -diversity per elevational belt by counting all the species collected within belts (hereafter α_e) and second, we calculated α -diversity at local scale by averaging the number of species collected within quadrat for each belt (hereafter α_q). However, using equivalent sampling effort in combination with the same standardized method along the elevational gradient may still result in differences in inventory completeness, therefore we assessed the inventory completeness for the two spatial scales by calculating the ratio of observed richness to the richness estimators first and second-order Jackknife (Jack1 & Jack2) at each elevation belt. Jack1 and Jack2 estimators have performed consistently well in comparisons of various estimators of species richness (Hortal et al. 2006) and provide reliable estimates of local species richness of plant species even when habitats are heterogeneous within sampling units (González-Oreja et al. 2010). The completeness values are given in Appendix S1 and Pearson's correlation between observed and estimated species richness are presented in Appendix S2. Since observed species richness values were highly correlated with species values

estimated with both Jack1 and Jack2, and since we did not find any strong variation across belts for species completeness, we considered that the species inventories were comparable across the elevational gradient.

We defined β -diversity as the dissimilarity in species composition between pairs of elevation belt and as the mean dissimilarity in species composition between pairs of quadrats within belts. We used the method of Carvalho et al. (2012) (see also Podani & Schmera 2011) to decompose the β -diversity in two components: species replacement and species richness difference. The species replacement indicates that one or more species are substituted by different species between sites, while species richness difference refers to the absolute differences in species richness (loss and gain) between sites. The two components are therefore additive and can be generally defined as:

$$\beta_{\text{total}} = \beta_{\text{repl}} + \beta_{\text{rich}}$$

Analytically, the β -diversity β_{total} between sites (herein, either between elevation belts or between quadrats) was quantified by the Jaccard similarity index:

$$\beta_{\text{total}} = (b + c)/(a + b + c)$$

with a , the number of species common to both sites, b the number of species exclusive to the first site, and c the number of species exclusive to the second site. β_{total} is bounded between 0 (the two sites have exactly the same species) and 1 (dissimilarity originated by species replacement and/or species richness difference is maximal). β_{total} can be further partitioned into its replacement components defined as follows:

$$\beta_{\text{repl}} = 2 * ((\min(b, c))/(a + b + c))$$

where $\min(b, c)$ is the minimum number of exclusive species. This quantity is multiplied by two because each substitution involved two different species.

The absolute species richness difference between sites is defined as follows:

$$\beta_{\text{rich}} = |b - c|/(a + b + c)$$

where $b - c$ is the absolute difference between the number of exclusive species in both sites. The value of β_{rich} also varies between 0 and 1.

Data analysis

In this study, we only used elevation as the ecological gradient since this gradient was highly correlated with the

different environmental variables measured in the course of our study (temperature, humidity, tree, shrub and herb cover and elevation belt area; all Pearson's correlations >0.8 , data not shown).

Our first set of analyses aimed to test how α - and β -diversity, at the two spatial scales, vary along the elevational gradient. For α -diversity, we used ordinary-least-square models (OLS) for both α_e and α_q . We first fit a simple linear model including elevation as a unique predictor and in a second model we included a quadratic term (elevation²) to highlight potential hump-shaped patterns with elevation. The significance of both models was assessed using the F -statistic and model fits were described by adjusted R^2 values. In addition, we defined an appropriate null model as an OLS model with intercept only to highlight a potential absence of relationship. These three models (linear, quadratic and intercept only) were further compared between each other using the small sample size-corrected AICc, the best model being the one with the lowest AICc. However, all models with a Δ AICc value < 2 were considered as receiving equal statistical support (Burnham & Anderson 2002). Residuals of the best models were surveyed in order to detect deviations from normality and homoscedasticity and to identify outliers. No specific deviations and outlier were detected. Following Foord & Dippenaar-Schoeman (2016) and for all β -diversity measures (β_{total} , β_{repl} and β_{rich} at the two spatial scales), relationships with elevation were modelled using binomial GLM. We implemented our Binomial GLMs by adopting a Quasi-likelihood approach to correct for overdispersion (Zuur et al. 2009). Specifically, for β -diversity between pairs of elevation belts, the relationship with elevation was evaluated against the differences in elevation between pairs of belts (hereafter elevation distance). As specified for α -diversity, we compared the performance of the three models described above (i.e. linear, quadratic and intercept

only) using Quasi-Akaike information criterion corrected for small sample size – (QAICc). The significance of both linear and quadratic GLMs was assessed using χ^2 statistics comparing each model to the intercept-only model and model fits were described by Efron's pseudo- R^2 . For both α - and β -diversity, if significant hump-shaped relationships were detected, we estimated the elevation E_{max} at which the diversity is expected to be maximum as $-S_1/2S_2$ with S_1 the slope estimated for elevation and S_2 the slope estimated for elevation². CI at 95% for E_{max} were estimated using a bootstrap resampling process.

The second set of analyses aimed to compare the contribution of species replacement and richness difference between and within elevation belts. We tested the difference between spatial scales for each β -diversity component separately (β_{total} , β_{repl} and β_{rich}) using Mann-Whitney-Wilcoxon tests. We tested the difference between β_{repl} and β_{rich} components within spatial scale using Wilcoxon signed-rank test for paired samples.

Statistical analyses were implemented within the R programming environment v 3.1.2. (R Foundation for Statistical Computing, Vienna, AT) using the package BAT (Cardoso et al. 2015) vegan, MuMIn and boot.

Results

Floristic results

A total of 121 species (89 mosses and 32 liverworts; 112 terrestrials and 45 epiphytes), a little more than one-third (35.17%) of the bryophytes of La Palma, were found along this elevational transect. Pottiaceae was the most diverse family with the largest number of genera represented (ten genera and 20 species), followed by Brachytheciaceae (eight genera and 14 species), and Lejeuneaceae (four genera and seven species). No liverwort species were found above 1400 m (see Fig. 2).

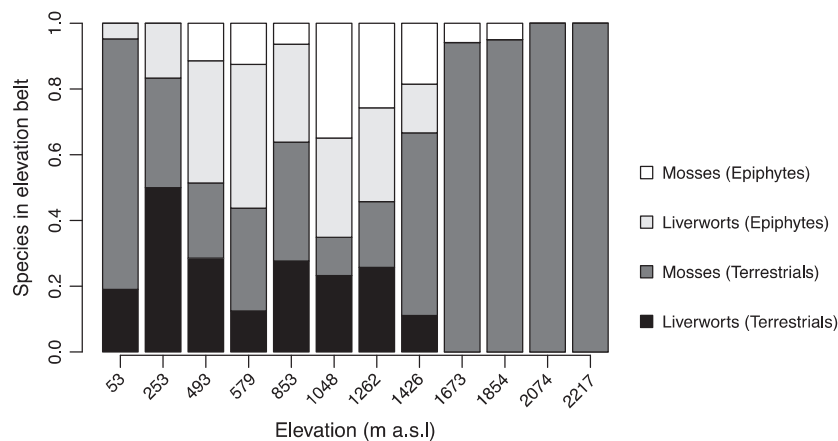


Fig. 2. Proportion of species of the four groups considered in each elevation belt of 200 m.

Alpha- (α) diversity along the elevational gradient

For all groups, we observed a strong and positive relationship between α for elevation belt (α_e) and mean α between quadrats (α_q) within elevation belt (All Pearson's correlation, $r > 0.86$; see Appendix S2). Regarding the relationship with elevation (Fig. 3), we found a significant hump-shaped pattern at the two spatial scales for all bryophytes, liverworts and epiphytic species (i.e. quadratic OLS with $\Delta\text{AICc} = 0$ and linear and intercept-only OLS with $\Delta\text{AICc} > 2$). The R^2_{adj} for the quadratic OLS was high, ranging from 0.593 for α_q of all bryophyte species to 0.867 for α_e of liverworts (See Appendix S3). Expected maximum species richness E_{max} did not show any specific differences between spatial scales and between groups for all bryophytes, liverworts and epiphytes (Table 1). For the two remaining groups, namely mosses and terrestrial species, we found an absence of relationship with elevation at both scales (i.e. intercept-only OLS with $\Delta\text{AICc} = 0$ and linear and quadratic OLS with $\Delta\text{AICc} > 2$).

Beta- (β) diversity along the elevational gradient

For β -diversity patterns between pairs of elevation belts and regardless of the groups considered, β_{total} showed a clear increase with elevational distance (Fig. 4) with a quadratic GLM as the best model for all bryophytes and the linear GLM as the best model for the four other groups (Fig. 4, Appendix S4). However, in all cases, we found substantial model uncertainty between linear and quadratic models ($\Delta\text{AICc} < 2$ between both models, see Appendix S4). Pseudo- R^2 ranged from 0.219 for liverworts to 0.377 for mosses (Appendix S3). Species replacement β_{repl} showed a clear increase as elevational distance increased for all bryophytes (Pseudo- $R^2 = 0.086$), mosses (Pseudo- $R^2 = 0.136$) and liverworts (Pseudo- $R^2 = 0.432$) although model uncertainty was detected between a linear

Table 1. Values of E_{max} for α -diversity indicating the elevation at which the diversity is expected to be maximal. Values of bootstrapped CI at 95% is given in square brackets. Values of E_{max} are given only for the groups that displayed significant hump-shaped relationships with elevation.

	$E_{\text{max}} \alpha_e$ (m a.s.l.)	$E_{\text{max}} \alpha_q$ (m a.s.l.)
All Bryophytes	968 [700; 1106]	984 [383; 1079]
Liverworts	795 [762; 983]	799 [739; 977]
Epiphytes	934 [812; 1027]	914 [637; 995]

and quadratic model for the first two (Appendix S4). For terrestrial species, β_{repl} showed a clear hump-shaped patterns with elevation (Pseudo- $R^2 = 0.168$) with a E_{max} at 1248 m a.s.l. [1078, 1908] (Table 1) while for epiphytic species β_{repl} displayed an inverse pattern (Pseudo- $R^2 = 0.220$) with a minimum β_{repl} reached at 804 m a.s.l. [635, 986]. For β_{rich} , we found no relationship with elevation distance for all groups except epiphytic species for which β_{rich} showed a clear hump-shaped pattern with elevational distance with an E_{max} at 926 m a.s.l. [809, 1269]. Overall, β_{total} was high along the gradient.

For mean β -diversity between quadrats within elevation belts, we did not find any significant relationship with elevation, regardless of the beta components (β_{total} , β_{repl} and β_{rich}) and the group considered except for β_{total} , which was found to increase with elevation (Pseudo- $R^2 = 0.744$) with the linear model as best model (Appendix S4). Overall, β_{total} was also high (Table 2). For all bryophytes, mosses and terrestrial species, species replacement was the most important contributor to β_{total} with β_{repl} significantly higher than β_{rich} (Wilcoxon signed-rank test, $P < 0.05$). In contrast, no differences were found between β_{repl} and β_{rich} for liverworts and epiphytic species ($P > 0.05$; Table 2, Appendix S5).

The comparisons of β -diversity values between the two spatial scales, β_{total} and β_{repl} showed higher values between elevation belts than between quadrats within belts for all

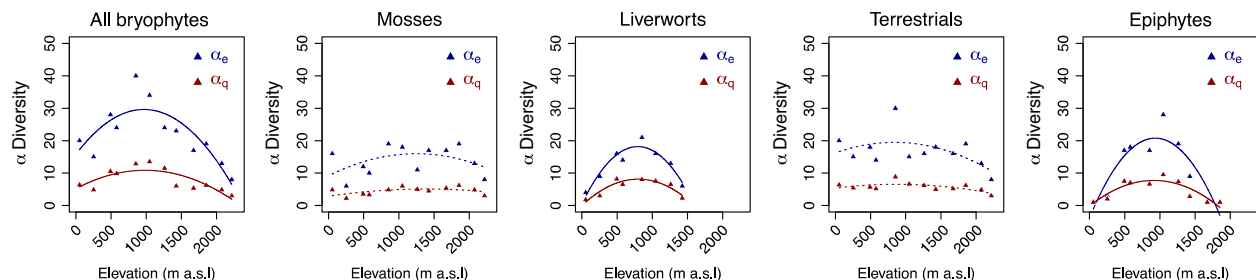


Fig. 3. Response plots of α -diversity to the elevational gradient in La Palma Island (Canary Islands) for all bryophyte species together and each of the four groups considered in the study: mosses, liverworts, terrestrials and epiphytes. Alpha-diversity was calculated at two different scales: at the elevation belt scale where the total number of species was calculated (α_e) and at local scales (quadrat), where mean α -diversity was calculated by averaging species richness between quadrat (α_q). Solid lines indicate significant relationship between α -diversity and elevation while dashed lines indicate non-significant relationships.

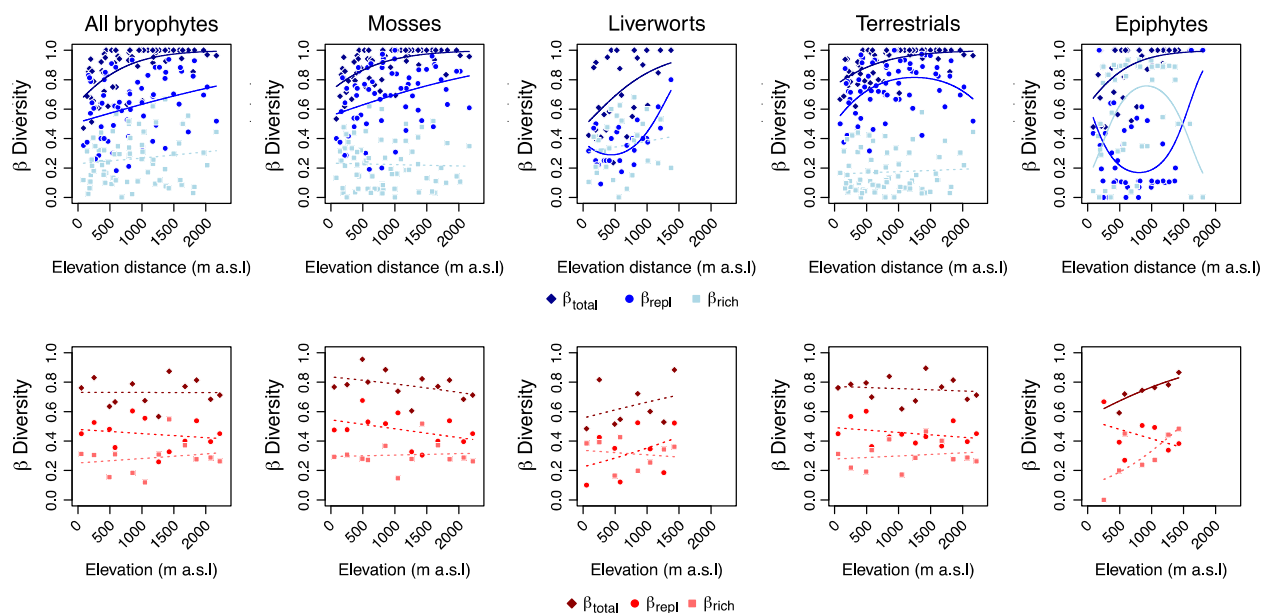


Fig. 4. Response plots of β -diversity to the elevational gradient in La Palma Island (Canary Islands) for all bryophyte species together and for each of the four groups considered in the study: mosses, liverworts, terrestrials and epiphytes. Top panels represent β -diversity calculated between pairs of belt of 200 m against elevational distance. Bottom panels represent mean β -diversity calculated between quadrats within belts of 200 m range against elevation gradient. For both cases, β -diversity was measured using the Jaccard's index (β_{total}) and further partitioned in species replacement (β_{repl}) and species richness (β_{rich}) components. Solid lines indicate significant relationship between β -diversity and elevation while dashed lines indicate non-significant relationships.

Table 2. Mean values of β -diversity and its associated SD between quadrats within elevation belts and between elevation belts for β_{total} and its replacement (β_{repl}) and species richness (β_{rich}) components for the different phylogenetic and ecological groups considered.

	β_{total}	β_{repl}	β_{rich}
Between Elevation Belts			
All Bryophytes	0.88 ± 0.15	0.61 ± 0.21	0.26 ± 0.16
Mosses	0.90 ± 0.11	0.68 ± 0.21	0.22 ± 0.16
Liverworts	0.71 ± 0.25	0.36 ± 0.16	0.35 ± 0.19
Terrestrials	0.91 ± 0.11	0.74 ± 0.17	0.17 ± 0.14
Epiphytes	0.87 ± 0.17	0.3 ± 0.27	0.57 ± 0.35
Within Quadrats Between Elevation Belts			
All Bryophytes	0.73 ± 0.09	0.44 ± 0.10	0.29 ± 0.11
Mosses	0.78 ± 0.09	0.47 ± 0.11	0.30 ± 0.09
Liverworts	0.64 ± 0.15	0.32 ± 0.17	0.32 ± 0.10
Terrestrials	0.75 ± 0.08	0.45 ± 0.08	0.30 ± 0.09
Epiphytes	0.73 ± 0.09	0.44 ± 0.13	0.30 ± 0.17

bryophytes, mosses and terrestrial species (Fig. 5, Mann–Whitney–Wilcoxon test, $P < 0.05$), while no significant differences were reported for β_{rich} ($P > 0.05$). For liverworts species, no significant differences were reported between scales for β_{total} , β_{repl} and β_{rich} . For epiphytic species, both β_{total} and β_{rich} were higher between elevation belts ($P < 0.05$) while no difference was found for β_{rich} between scales ($P = 0.08$).

Discussion

This is the first study to evaluate bryophyte α - and β -diversity composition at two different spatial scales across an elevational gradient in an oceanic island. In general, it shows that bryophyte diversity was influenced by spatial turnover at the largest scale.

Our results showed that α -diversity among elevational levels (α_e) was always higher than α -diversity at the quadrat scale (α_q), being the largest contributor to the overall species richness of the gradient. This pattern can be explained by the fact that the plots at each elevation were selected in the same type of forest, and with similar composition of vascular plants, so the largest variation in bryophyte species richness is produced by differences in elevation that are related to higher habitat heterogeneity along the elevation gradient. Low values of α -diversity at the smallest spatial scale have been observed in other studies with bryophytes (e.g. Caners et al. 2013) in which lower than expected α may be attributable to intraspecific aggregation, which occurs when individuals are associated with other individuals of the same species (Veech 2005).

Patterns of variation in diversity distribution along the elevational gradient showed some differences when considering different phylogenetic/ecological groups. For all bryophytes together, liverworts and epiphytic species, a

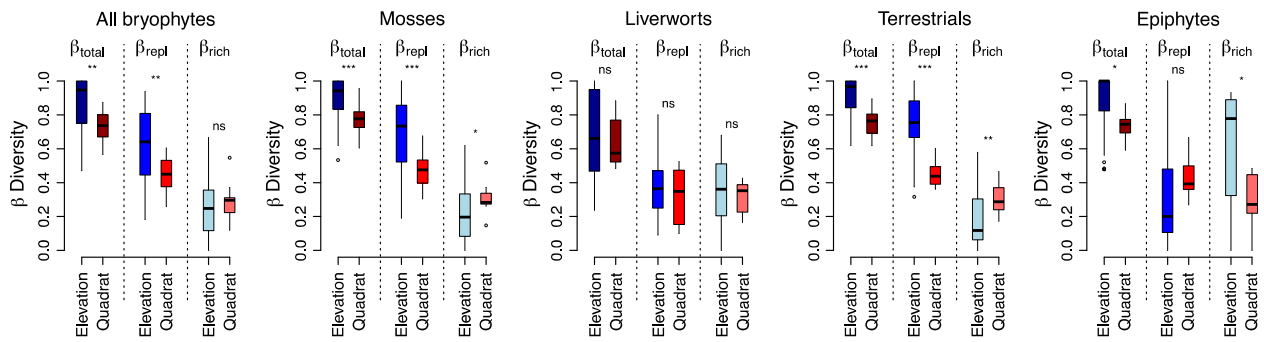


Fig. 5. Differences in β -diversity between measures calculated between elevation belt and measures between quadrat within belt of 200 m in La Palma Island (Canary Islands) for all bryophyte species together and for each of the four groups considered in the study: mosses, liverworts, terrestrials and epiphytes. Comparisons were assessed for the β -diversity measured with the Jaccard's index (β_{total}) and for its two components: species replacement (β_{repl}) and species richness (β_{rich}). Results of the Wilcoxon test performed to test differences in β -diversity between scales are indicated on the top part of each pair of boxplots with * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ and ns non-significant.

hump-shaped pattern of α -diversity was observed, while for mosses and terrestrials no significant relationship was found. The mid-elevational peak in species richness was also observed elsewhere in bryophytes (Ah-Peng et al. 2012; Henriques et al. 2016) and ferns (Kessler et al. 2011). The absence of a clear pattern of α -diversity for mosses and terrestrials may be explained by the fact that these groups are not so highly dependent on the humidity conditions as are epiphytes and liverworts. In addition, higher humidity conditions at middle elevations result in an increase of species richness that may also be influencing the patterns observed. Liverworts are known to be a group that are highly dependent on moisture conditions (e.g. Gabriel & Bates 2005; Lloret & González-Mancebo 2011), which results in a higher β -diversity in this group in comparison with mosses, since lower and higher margins of the forests (with lower humidity conditions than in the intermediate forest elevations) result in highly divergent communities among similar habitats. For epiphytic bryophytes (including a high proportion of liverworts in our transect), it is accepted that bryophyte communities vary as a function of the host species and the specific environmental conditions (González-Mancebo et al. 2003; Gabriel & Bates 2005; Patiño & González-Mancebo 2011), so composition of vascular plants (host) will determine epiphytic community composition. At middle elevation, great heterogeneity of hosts is found within quadrats, which may promote an increase in α -diversity for epiphytes in the mid-part of the gradient, where more complexity in microhabitats exists, favouring the presence of more and different species of both liverworts and epiphytes. Other studies of bryophytes along elevational gradients on the Canary Islands showed the importance of the altitudinal range of cloud belts for the distribution of phylogenetic groups highly dependent of humidity conditions (Lloret & González-Mancebo 2011). On the other hand, mosses and

terrestrial species richness remained relatively homogeneous along the whole gradient, since they are not strongly affected by these special requirements and can easily colonize microhabitats that are present at any elevation. The common justification of water limitation at low altitude and low temperature at high altitude for the hump-shaped pattern is consequently not a valid explanation for bryophytes, since diversity of mosses and terrestrial species was not affected in the studied gradient, although the proportions between groups shows the mentioned elevational restrictions for liverworts and epiphytes. Therefore, our results show that groups with different ecological and physiological requirements show different diversity patterns along the elevational gradient.

Beta-diversity patterns are determined by two basic processes: the replacement of species and richness difference (Carvalho et al. 2012, 2013). Species replacement (i.e. true turnover) is thought to be the consequence of environmental sorting, or spatial and historical constraints (Qian et al. 2005); it is particularly important for species that are strongly associated with their environment such that changes in environmental attributes will result in changes in species composition (López-González et al. 2015). Along our studied elevational gradient, compositional differences attributable to replacement were significantly higher than compositional differences attributable to richness differences for all bryophytes, mosses and terrestrial species. The geological old age of La Palma, its relatively large area and high habitat diversity, driven by contrasting topography and a large temperature and humidity gradient, provides a wealth of habitat types, generating an important percentage of species replacement. This has also been found in other taxonomic groups, for instance for spiders in a multi-sites study across Macaronesian archipelagos (Azores, Selvagens and Madeira; Carvalho & Cardoso 2014). Our study thus supports the role of habitat

specialization for bryophytes and suggests that all sites should be potential targets for conservation.

The methods applied here revealed both strong differences along the elevational gradient, related to replacement, and differences between phylogenetic and ecological groups, dependent on climatic conditions and substrate availability. Our results also show the importance of including different phylogenetic groups to infer conclusions about the role of the ecological factors on biodiversity distribution. In addition, by investigating different scales and observing differences for β -diversity decomposition is more informative than looking at α -diversity pattern along the elevational gradient alone. This study contributes to the understanding of the spatial organization of bryophyte diversity at multiple scales along a major elevational gradient and the roles of spatial organization, climate and vegetation in shaping this diversity. An additional value of these results is the use of the same standardized sampling method, which represents a hierarchical design along elevational gradients, across a variety of oceanic islands within the MOVECLIM project (Ah-Peng et al. 2014; Gabriel et al. 2014), which will ultimately contribute towards better understanding the factors affecting α - and β -diversity at varying spatial scales.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Values of α diversity and sampling completeness at each elevation belt of 200 m.

Appendix S2. Pearson's correlation between observed species richness and species estimated with Jack1 and Jack2 two different scales: for elevation belt scale and at local scales (quadrat).

Appendix S3. Results of the model selection performed to identify the form of the relationship between α -diversity and the elevation gradient.

Appendix S4. Results of the model selection performed to identify the form of the relationship between β -diversity and the elevation gradient.

Appendix S5. Differences in the β -diversity between the components species replacement (β_{repl}) and species richness (β_{rich}).