

DR. STEFFEN BOCH (Orcid ID : 0000-0003-2814-5343)

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Hans Henrik Bruun

Bryophyte and macrolichen diversity show contrasting elevation relationships and are negatively affected by disturbances in laurel forests of Madeira island

Running title: Bryophyte and lichen richness on Madeira

Steffen Boch^{1*}, Anabela Martins², Sara Ruas², Susana Fontinha^{3,4}, Palmira Carvalho², Fábio Reis⁴, Ariel Bergamini^{1#}, Manuela Sim-Sim^{2,3#}

¹ WSL Swiss Federal Research Institute, Birmensdorf, Switzerland

² cE3c - Centre for Ecology, Evolution and Environmental Changes, Natural History and Systematics (NHS) Research Group /MUHNAC - Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Lisboa, Portugal

³cE3c, Centre for Ecology, Evolution and Environmental Changes, Universidade de Lisboa, Faculdade de Ciências, Lisboa, Portugal

⁴ Banco de Germoplasma ISOplexis, Universidade da Madeira, Funchal, Portugal.

#These authors contributed equally to this work and share the last authorship

*corresponding author: steffen.boch@wsl.ch

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Author contributions

A.B. and M.S.S. conceived and designed the project. A.B., F.R., P.C., S.R., S.F. conducted the field work. A.B., A.M., M.S.S., S.B. analyzed the data. S.B. wrote the first draft of the paper. All authors contributed to the final manuscript.

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Data accessibility statement

Primary data is available from A.B. (ariel.bergamini@wsl.ch).

Conflict of Interest

We have no conflict of interest to declare.

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Abstract

Questions

Studies on bryophyte and lichen diversity patterns along elevational gradients are scarce, although this approach can serve as space-for-time substitution to predict diversity changes because of climate warming. Therefore, we investigated bryophytes and macrolichens in disturbed and undisturbed stands along an elevational gradient in the unique laurel forest of Madeira island by addressing the following questions: (1) How does the species richness of functional-taxonomic bryophyte and macrolichen groups differ with elevation? (2) How is the species richness of these groups affected by disturbances?

Location

UNESCO World Natural Heritage site laurel forest of Madeira island (Madeira, Portugal).

Methods

We analyzed species richness of bryophytes and macrolichens in 92 plots in response to elevation and to disturbances.

Results

Bryophytes species richness showed a mid-elevational peak, while macrolichen richness was increasing with elevation. Disturbed plots harbored on average 20% less bryophyte and macrolichen species than undisturbed plots.

Conclusions

The laurel forest of Madeira is a bryophyte and lichen diversity hotspot. Our findings indicate future biodiversity threats by changing environmental conditions. This calls for the need of a strict protection status for the laurel forest on Madeira to minimize human-related disturbances, the development of management measures that could mitigate climate change effects by maximizing habitat suitability and for the implementation of species-conservation programs to prevent future extinctions, in particular of endemic species.

Keywords

Elevational gradient; bryophyte life strategy; climate change; endemic species; functional-taxonomic group; lichen growth form; liverwort; moss; photobiont

Introduction

Mountain ecosystems harbor a rich biodiversity, are particularly sensitive to ecological changes and currently experience the highest impacts of human-induced climate change (Gobiet et al. 2014). Increasing temperatures can change climatic conditions and thereby affect mountain biodiversity, lead to species shifts towards higher elevations, or promote extinctions of high-elevation plants (Payne, Spehn, Snethlage, & Fischer 2017). In addition to increasing mean temperatures, the climatic variability and temperature extremes might increase in future (Schär et al. 2004), having severe effects on plants (Reyer et al. 2013).

Elevational gradients have been widely used as space-for-time substitution approach in mountain-biodiversity studies to investigate the effects of climate-warming. In particular, warmer low-elevation sites indicate future climatic conditions of colder high-elevation sites. Therefore, low sites might mirror the potential future species composition of high elevation

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sites, if species manage to colonize higher areas (Payne et al. 2017). Species richness-elevation relationships are well explored, with a mid-elevational peak being the most common relationship (McCain & Grytnes 2010). However, relationships are differing among taxa and are affected by climatic, spatial, biotic and evolutionary factors (Rahbek 2005; McCain & Grytnes 2010; Boch et al. 2019).

Disturbances are important drivers of forest ecosystem dynamics, and modulate the structure of forest ecosystems (Bengtsson, Nilsson, Franc, & Menozzi 2000). According to the intermediate disturbance hypothesis, the highest species richness is expected at intermediate disturbance levels (Connell 1978). While vascular plant species richness is largely promoted by disturbances in European forests, the effects on the diversity of other taxa, such as bryophytes and lichens, are less well explored and seem to differ among regions and ecosystems (e.g. Paillet et al. 2010; Boch, Prati, Hessenmöller, Schulze, & Fischer 2013a). Whether ongoing climatic changes will increase the frequency and severity of disturbances and whether this will negatively affect forest biodiversity is still unclear (Braunisch et al. 2014).

In Europe and the Macaronesian region, the Madeira Archipelago is a biodiversity hotspot. Its main forest formation, the laurel forest (Laurisilva), covers approximately 20% (15,000 ha) of Madeira. It occurs essentially on the north coast, mainly between 300 and 1450 m a.s.l. where precipitation and humidity are high. Because of its unique biodiversity, including many endemic species, this forest type is considered as priority habitat in Annex I of the European Habitats Directive (92/43/EEC). It was further designated as part of the Natura 2000 network and as UNESCO World Natural Heritage site. Climate projections for Madeira indicate an average temperature increase of up to 3°C and an annual precipitation decrease of

about 30% until 2100. This may shift the distribution of the natural forest to higher elevations and constitute a future biodiversity threat (Gomes, Avelar, Duarte Santos, Costa, & Garret 2015; Patiño et al. 2016).

Bryophytes and lichens are important components of the biodiversity in various ecosystems where they cover soil, rocks and the bark of trees (Boch, Müller, Prati, Blaser, & Fischer 2013b; Boch, Müller, Prati, & Fischer 2018a). However, only little is known about bryophyte and macrolichen density in Madeiras' forests compared to other European regions. Beside the majority of widely distributed bryophyte and lichen species, there are also endemic species (Patiño & Vanderpoorten 2018). For example, the Madeiran laurel forest harbors 39% of all endemic bryophyte species of Macaronesia (Sim-Sim et al. 2014). Many bryophyte and lichen species are characterized by narrow ecological niches with specific requirements concerning substrate or habitat, and therefore react very sensitive to environmental, land-use and climatic changes. Because of their sensitivity, bryophytes and lichens are useful indicators to study the effects of environmental changes (Gignac 2001; Lloret & González-Mancebo 2011; Boch et al. 2018b). However, despite their suitability as sensitive indicators, studies assessing the species richness of bryophytes and lichens, including different substrates and covering an elevational gradient are scarce (but see Bergamini, Ungricht, & Hoffmann 2009; Bässler et al. 2016; Henriques, Borges, Ah-Peng, & Gabriel 2016, Hernández-Hernández et al. 2017; Nascimbene & Spitale 2017) and missing for Madeira island. Therefore, we investigated bryophyte and macrolichen species richness in disturbed and undisturbed stands along a laurel to tree-heath forest elevational gradient on Madeira island.

Our main questions are:

- (1) How does species richness of functional-taxonomic bryophyte and macrolichen groups differ along an elevational gradient on Madeira?
- (2) How are disturbances affecting the species richness of functional-taxonomic bryophyte and macrolichen groups?

Methods

Study area

Madeira Island is a within-plate volcanic island and belongs to the Archipelago of Madeira (Portugal). It is situated in the Atlantic Ocean, approximately 600 km northwest of the Western African coast. The northern slopes of Madeira island are characterized by high precipitation because the island forms a natural barrier for trade winds from the northeast which transport humid maritime air. Condensation effects lead to a fog cover of these northern slopes, extending 200 days per year and resulting in a maximum annual precipitation of almost 3000 mm (Prada, Sequeira, Figueira, & Silva 2009).

This climatic phenomenon is the reason for the unique vegetation on the northern slopes: the outstanding Mediterranean laurel and stink-laurel forest communities (*Semele androgynae-Apollonio barbujanae* and *Clethro arboreae-Ocoteo foetentis*). Fifteen to forty million years ago, this forest type was widespread in Southern Europe. On Madeira, large parts are considered primary forest. At elevations of 600 to 800 m a.s.l., shrubs from tree-heath communities admix with the laurel forest, which is then gradually changing to tree-heath forests dominated by *Erica* species and *Morella faya* (*Vaccinio padifoli-Ericetum maderincolae* and *Polysticho falcinelli-Erico arboreae*), growing up to 1650 m a.s.l. (Capelo, Sequeira, Jardim, Mesquita, & Costa, 2005).

Sampling design and plot data

Our sampling area comprised the full extent of the laurel forest, including the transition zone to the tree heath forest at its upper elevational limit. We selected our study sites from the intersection points of a 500 m grid, resulting in a total of 639 possible central sites. In every direction (N, E, S, W) of each site, we selected four satellite sites in a distance of 100 m. In ascending order, we assessed the central and satellite sites and discarded sites with a slope $>60^\circ$, which were inaccessible (e.g. steep cliffs), with a tree cover $<20\%$ or plantations of non-native tree species (e.g. *Eucalyptus*, *Acacia*, *Pinus*). We finally surveyed 92 sites, which were evenly distributed along the elevational gradient (29 plots below 600 m, 30 plots between 600 and 900 m and 33 plots above 900 m; Fig. 1).

Between 2011 and 2013, we established a circular plot of 100 m^2 (radius 5.64 m) at each site. The centre of each plot was permanently marked belowground with a metal pole to ensure future relocation. Within each plot, we further selected four $1\times 1\text{ m}$ subplots on the forest floor including substrates such as soil, litter, humus, deadwood and rocks. The first subplot was placed in the center of the 100 m^2 plot, the second 5.64 m northwards from the plot center, the third at 120° , and the fourth at 240° , in clock-wise direction from the second subplot and at 5.64 m from the plot center. In addition, we selected two trees with a diameter at breast height (DBH) of at least 6.4 cm (for details see Appendix S1). On the stems of each tree, we placed two rectangle subplots of $160\times 10\text{ cm}$ in the directions NNW (30°) and SSE (210°). Within each subplot, we sampled all bryophyte (mosses, liverworts, hornworts) and macrolichen species (i.e. excluding crustose species) from all substrates. We are aware that sampling only four 1 m^2 subplots on the ground and two subplots on each of the two trees does not represent the total species richness of a plot. However, given the very laborious

sampling because of the high species richness we had to limit the survey effort in favor of a larger sample size.

For each plot, coordinates and elevation were measured. In addition, we distinguished disturbed (N = 65) and undisturbed (N = 27) plots based on visible signs evaluated by Susana Fontinha, a local expert of the secretariat for the environment and natural resources of Madeira island. Beside natural disturbances such as landslides (8 plots), various historic human-related disturbances were still visible comprising burnings (41 plots), former pastures (32 plots) or agricultural activities (19 plots) and logging (4 plots), although all plots were situated in the protected area of the Madeira Natural Park (for details see Appendix S1).

Bryophyte and macrolichen data

Nomenclature of bryophytes and classification of Macaronesian endemics follows Ros et al. (2007) for liverworts and hornworts, Patiño, Devos, Vanderpoorten, Schäfer-Verwimp, and Renner (2013) for *Radula carringtonii*, Ros et al. (2013) for mosses and Patiño et al. (2017) for *Rhynchostegiella* spp. Red list status of bryophyte species is based on Sim-Sim et al. (2014). Nomenclature of macrolichens follows Clauzade and Roux (1985) and Smith et al. (2009). For lichen species no Red List exists for Madeira. Nomenclature of vascular plants follows (Euro+Med 2006–2019). Life strategy of bryophytes refers to During (1992) and was based on the BRYOTRAIT-AZO database (<http://islandlab.uac.pt/software/ver.php?id=26>), growth form and photobiont information of lichens were derived from Stofer et al. (2006) and complemented using Smith et al. 2009. For species that were only identified to genus level, we added values which are consistent within the particular genus (e.g. cyanobacterial photobiont for all *Leptogium* species).

Data analyses

All statistical tests were performed in R version 3.3.3 (R Core Team 2017).

We calculated the total species richness in each plot (cumulative number of subplots), of the forest floor, and the trees, separately for bryophytes and macrolichens. We further separated bryophytes into the two functional-taxonomic groups mosses and liverworts and calculated their species richness. As number and frequency of hornworts was low, we did not analyse them separately. In addition, we calculated the number of species by four different bryophyte life strategies: colonists, short-lived shuttle species, long-lived shuttle species and perennials. These groups are considered to differ in their ecological requirements and to react differently to habitat changes (e.g. disturbances: During 1992; climate: Lloret & González-Mancebo 2011). Finally, we calculated the number of Red List and endemic bryophyte species per plot.

We separated macrolichens into functional groups based on their vegetative traits. The first group separates species by their photobiont (green algae vs. cyanobacteria), the second group separates species by their growth form (foliose adpressed, foliose ascendant, fruticose erect, fruticose pendulous). We then calculated the number of species per group and plot. These functional groups are considered reacting differently to habitat changes and show preferences to different habitat conditions (Stofer et al. 2006).

We analyzed the species richness in response to elevation using regression models. As we suspected non-linear relationships between species richness and elevation, we also included elevation as quadratic term and omitted it if not significant. We square-root transformed the number of red list species to better fit the normal distribution of the residuals. We further tested the effect of disturbances (y/n) on species richness using Wilcoxon tests. Disturbances were not related to elevation (one-way anova, $p = 0.797$).

Results

Bryophyte and macrolichen species richness

We found a total of 198 bryophyte species (108 mosses, 89 liverworts, 1 hornwort). Of these, 189 were growing in the forest floor subplots (82 exclusively on the forest floor) and 117 on trees (9 exclusively on trees). 26 species were Macaronesian endemics (Appendix S2). On average we found 27.6 (± 1.1 SE) bryophyte species per plot. Of these, 16.6 (± 0.7) were liverworts and 11.0 (± 0.5) mosses. 3.3 (± 0.3) species per plot were Macaronesian endemics.

We found 101 macrolichen species, of which 66 contained a green-algal and 35 a cyanobacteria photobiont. 98 were growing on the forest floor (17 exclusively on the forest floor) and 83 on trees (3 exclusively on trees; Appendix S3). On average we found 9.6 (± 0.8) macrolichen species per plot.

Relationship between bryophyte species richness and elevation

Bryophyte species richness as well as the richness of species on the forest floor and on trees followed an optimum curve along elevation, peaking at 939 m, 981 m and 944 m a.s.l., respectively (Fig. 2, Tab. 1). This pattern was also true for endemic bryophytes with a species richness peak at 870 m a.s.l, as well as for mosses and liverworts peaking at 878 m and 961 m a.s.l. Bryophyte life strategy groups responded differently to elevation: While the richness of long-lived shuttle species and of perennials showed a hump-shaped relationship with elevation peaking at 866 m and 980 m a.s.l, the richness of colonists showed no relationship with elevation and the richness of short-lived shuttle species was slightly linearly increasing (Fig. 2). There was no relationship between the richness of Red list species and elevation (Tab. 1).

Relationship between macrolichen species richness and elevation

The richness of macrolichen species, as well as the one of the different functional-taxonomic groups was increasing with elevation. On average, macrolichen species richness was increasing by 1.58 species per 100 m of elevation (Tab. 2; Fig. 3).

Disturbance effects on bryophyte species richness

Bryophyte species richness was 20% lower in disturbed than in undisturbed plots (Tab. 3, Appendix S4). The richness of mosses, colonists, short-lived shuttle species, as well as red listed bryophyte species was not affected by disturbances, but the richness of liverworts and endemic bryophyte species was 24% and 48% lower in disturbed plots (Tab. 3, Appendix S4). The effects of disturbances on the species richness of the different functional-taxonomic groups on the plot level were mainly mediated by the effects on bryophyte species on the forest floor (28.1 ± 1.72 SE in undisturbed vs. 21.8 ± 1.28 in disturbed stands; Tab. 3), as the species richness of epiphytic bryophytes was only little affected (15.0 ± 1.10 in undisturbed vs. 12.5 ± 0.84 in disturbed stands). However, in disturbed plots epiphytic liverwort and endemic bryophyte species richness was 20% and 51% lower than in undisturbed plots (Tab. 3).

Disturbance effects on macrolichen species richness

Macrolichen species richness was 22% lower in disturbed than in undisturbed plots. In particular, disturbed plots harbored 20% less green-algae and 27% less cyanobacteria species (Tab. 3, Appendix S4), as well as 29% less foliose adpressed and 35% less foliose ascendant species (Tab. 3). The richness of the two fruticose lichen groups was not affected by disturbances. Disturbance effects slightly differed between cyanobacteria species on the

forest floor and on trees: while forest floor species were not affected, disturbed plots harbored 45% less epiphytic cyanobacteria macrolichens than disturbed plots (Tab. 3).

Discussion

Our findings highlight the laurel forest of Madeira as bryophyte and lichen diversity hotspot, which is threatened by changing environmental conditions as they are expected by future climate change. Moreover, legacy effects of former disturbances such as forestry or agricultural activities are still visible within the protected area by lower species richness within a range of groups, i.e. endemic bryophytes, pointing out the sensitivity of the system against disturbances.

Bryophyte and macrolichen species richness

Bryophyte and macrolichen richness per plot is quite high (as we only sampled 4 m² of forest floor and 0.64 m² of bark surface) compared with other regions (for lichens: Boch et al. 2013a; Nascimbene & Marini 2015; Cleavitt, Clyne, & Fahey 2019; for bryophytes: Horvat, Heras, Garcia-Mijangos, and Biurrun 2017 and Müller et al. 2019). We did not sample crustose lichen species, but as their richness is often much higher than the one of macrolichens and both diversities are positively correlated (Bergamini, Stofer, Bolliger, & Scheidegger, 2007), we assume that also the total lichen richness would exceed average values of most parts of other European countries. This and the occurrence of many endemic bryophytes highlights the outstanding conservational value of the laurel forest of Madeira as diversity hotspot of bryophytes and lichens.

Relationship of bryophyte and macrolichen species richness with elevation

The mid-domain effect was the major species richness-elevation relationship for bryophytes peaking around 900 m a.s.l. This pattern seems to be common for various taxa (Rahbek 2005). Thus, our findings are in line with other bryophyte species richness-elevation relationship studies: Ah-Peng et al. (2012) on Réunion Island and in Colombia, Grau, Grytnes, and Birks (2007) in Nepal, and Henriques et al. (2016) on the Azores found bryophyte richness peaking at mid elevations. The mid-domain effect can be explained by the overlap of distribution ranges of low- and high-elevation species and by favorable environmental conditions at intermediate elevation (e.g. climatic conditions are often harsher at low and high elevations than at intermediate elevations), promoting high speciation and low extinction (reviewed in McCain & Grytnes 2010). This is particularly true for the laurel forest on Madeira island (Capelo et al. 2005). Because the cover and biomass of macrolichens is strongly increasing with elevation (pers. observation), the decrease of bryophyte species richness from intermediate to high elevation areas might also be attributed to competitive exclusion of some bryophytes by fast-growing macrolichen species (Ruas, Bergamini, Carvalho, Fontinha, & Sim-Sim, 2015), which might be driven by changes in productivity and functional traits of the accompanying species (Soliveres et al. 2018). However, this assumption needs further exploration.

In contrast to Bruun et al. (2006) and Baniya, C.B., Solhøy, T., Gauslaa, Y., and Palmer (2010, 2012) reporting an unimodal relationship of lichen species richness and elevation, we found a linear increase of macrolichen species richness with elevation. This finding is in accordance with other studies investigating lichen species richness along elevational gradients in forest ecosystems, e.g. Cobanoglu and Sevgi (2009) in a *Cedrus* forest in Turkey, Nascimbene and Marini (2015) in northern Italy, Bässler et al. (2016) in a German low-

mountain range, Chongbang, Keller, Nobis, Scheidegger, & Baniya (2018) in Eastern Nepal, and Cleavitt et al. (2019) in the northeastern United States. This is probably a methodological issue as we, and the other studies reporting a linear increase in lichen species richness with elevation, sampled a local elevational gradient within forest ecosystems without exceeding the timberline. It is therefore likely that we sampled only the increasing part of the hump and missed the decreasing part. However, the linear increase of macrolichen species richness along the elevational gradient on Madeira island might be further explained by the climatic and structural differences between the tree-heath and the laurel forest. In boreal forests, Gauslaa, Lie, Solhaug, and Ohlson (2006) found that light availability seems to be a limiting factor for macrolichen growth under moist conditions. Also, Király, Nascimbene, Tinya, and Ódor (2013) highlighted that lichens are prone to low-light levels in temperate forests. In our plots, humidity is increasing with elevation (Capelo et al. 2005) but water supply is likely sufficient also in the low-elevation plots and likely no limiting growth factor for macrolichens. However, tree-heath forests are more open with better light conditions than laurel forests, i.e. light conditions of crown branches and stems of *Erica* spp. and *Morella faya* are similar. Because of this, many light-demanding macrolichens grow on the lower parts of stems in tree-heath forests but not in laurel forests. In addition, these light conditions might also be a reason for various epiphytic species persistently growing on the forest floor (e.g. fruticose pendulous *Usnea* species and large-lobed foliose *Lobaria*, *Pseudocyphellaria* and *Sticta* species) in tree-heath forests, but not in laurel forests.

Disturbance effects on bryophyte and macrolichen species richness

In contrast to previous studies reporting a positive effect of disturbances (bryophyte richness: Müller et al. 2019), no effect (bryophyte and lichen richness: Schall et al. 2018) or no consistent effect (negative effect on lichen and no effect on bryophyte richness: Paillet et al.

2010) on species numbers, disturbed plots harbored fewer species than undisturbed ones in this study. These contrasting findings might be on the one hand because disturbance effects vary among regions and ecosystems and on the other hand because effects vary among disturbance types. Using a finer grained and continuous disturbance measure including the landscape context (e.g. Cardoso, Rigal, Fattorini, Terzopoulou, & Borges 2013) might help to disentangle these effects in future studies.

Related to our findings of a higher richness in undisturbed stands, Patiño, González-Mancebo, Fernández-Palacios, Arevalo, and Bermudez (2009) found strong positive effects of forest age on the number of epiphytic bryophytes. As species richness of perennial and long-lived bryophytes and of groups depending on old-growth forest attributes (several liverworts, endemic bryophytes, foliose lichens, epiphytic cyanobacteria lichens) declined with disturbances, the conservation of undisturbed forest stands is of particular importance. This conclusion is in line with many other studies pointing out the conservational value of mature trees and old-growth forest attributes for the conservation of specialist species (e.g. Gustafsson, et al. 2004; Patiño et al. 2009; Boch et al. 2013a).

Implications for future climate change

Climate change scenarios project increasing mean temperatures, but also increasing climatic variability and more frequent temperature extremes (Schär et al. 2004). On Madeira, these changes will likely come along with a precipitation decrease (Gomes et al. 2015), which might remarkably negatively affect bryophyte and lichen diversity (Mazimpaka, Medina, Draper, & Lara 2009). Actually, many specialized species depend on constantly humid conditions of the closed laurel forest at intermediate elevations (e.g. drought sensitive liverworts, endemic bryophytes, long-lived species, perennials) or light and moist conditions

in the more open tree-heath forests at high elevations (macrolichen species). Similar to our study, Lloret & González-Mancebo (2011) showed that many perennial and long-lived species as well as liverworts rely on the stable and moist conditions of laurel forests, suggesting their particular sensitivity to changing environmental conditions and range shifts. In addition, it is likely that the seasonal climatic conditions might change in future. Longer drought periods or a decrease of fog and mist frequency in combination with increasing temperatures might threaten bryophyte species richness and in particular the desiccation-sensitive species (Medina et al. 2014). Also, Bässler et al. (2016) suggested that desiccation-sensitive lichen species with complex growth forms might be excluded from lichen communities if climate conditions at higher elevations become more similar, i.e. dryer, with the ones of lower elevations. As most of our observed macrolichen species have a complex growth form (foliose ascendant, fruticose erect, fruticose pendulous) and depend on humid conditions, a decreasing water supply might have severe effects on their richness and abundance. In addition, particularly endemic bryophyte species might suffer from future climate change on Madeira, as suitable growth habitats might decrease by 62 to 87% depending on the species. Six of the Macaronesian endemic species, including three Madeiran endemics from the laurel forest might even become extinct if no conservation actions will be taken (Patiño et al. 2016). Moreover, bryophyte and lichen diversity might be further threatened by likely increasing disturbances by forest fires because of reduced future precipitation (Kaufmann & Berg 2014).

Conclusions

Our findings highlight the outstanding conservational value of the laurel forest of Madeira as bryophyte and lichen diversity hotspot. However, as climate change might alter environmental conditions, this diversity might be threatened in the future. On the one hand,

this calls for the need of a strict protection status of the laurel forest on Madeira island and to minimize disturbances, for example by efficient and fast suppression of forest fires. On the other hand it implies to establish species conservation programs (Patiño et al. 2016), including the development of management measures that could mitigate climate change effects by maximizing habitat suitability as well as *ex-situ* cultivation of the most threatened and in particular of the endemic species as well as re-introduction approaches such as assisted migration to prevent future extinctions.

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Table 1: Summary of regression models separating the effect of elevation on the species richness of the different bryophyte functional-taxonomic groups. As we suspected non-linear relationships between species richness values and elevation, we included elevation also as quadratic term. We omitted the quadratic term if not significant. Significant differences are indicated by bold p-values at $P < 0.05$. The column "direction" indicates either positive, negative, hump-shaped, dip-shaped or non-significant (ns) relationships.

Species richness		Plot			Forest floor			Trees		
		Slope	p	Direction	Slope	p	Direction	Slope	p	Direction
All bryophytes	Intercept	-0.82	0.883		-1.07	0.843		-6.81	0.034	
	Elevation	0.07	<0.001		0.06	<0.001		0.05	<0.001	
	Elevation ²	-0.01	<0.001	∩	-0.01	0.001	∩	-0.01	<0.001	∩
Liverworts	Intercept	-5.17	0.130		-5.20	0.099		-6.17	0.010	
	Elevation	0.05	<0.001		0.04	<0.001		0.04	<0.001	
	Elevation ²	-0.01	<0.001	∩	-0.01	0.000	∩	-0.01	<0.001	∩
Mosses	Intercept	4.35	0.124		8.46	<0.001		-0.63	0.592	
	Elevation	0.02	0.023		0.01	0.282		0.01	0.004	
	Elevation ²	-0.01	0.035	∩	-	-		-0.01	0.021	∩
Endemics	Intercept	-1.30	0.340		-1.05	0.426		-1.81	0.057	
	Elevation	0.01	0.001		0.01	0.009		0.01	<0.001	
	Elevation ²	-0.01	0.002	∩	-0.01	0.017	∩	-0.01	<0.001	∩
Red List species	Intercept	0.42	0.030		0.35	0.053		0.16	0.260	
	Elevation	0.01	0.198	ns	0.01	0.378	ns	0.01	0.222	ns
Colonists	Intercept	5.98	<0.001		5.61	<0.001		0.86	0.006	
	Elevation	0.01	0.580	ns	0.01	0.627	ns	0.01	0.949	ns
Short-lived shuttle species	Intercept	0.28	0.345		0.13	0.577		0.21	0.344	
	Elevation	0.01	0.008	+	0.01	0.005	+	0.01	0.289	ns
Long-lived shuttle species	Intercept	-2.66	0.163		-3.71	0.039		-2.95	0.047	
	Elevation	0.03	<0.001		0.03	<0.001		0.02	<0.001	
	Elevation ²	-0.01	<0.001	∩	-0.01	<0.001	∩	-0.01	<0.001	∩
Perennials	Intercept	-3.71	0.194		-3.24	0.248		-3.77	0.023	
	Elevation	0.04	<0.001		0.03	<0.001		0.02	<0.001	
	Elevation ²	-0.01	<0.001	∩	-0.01	0.002	∩	-0.01	<0.001	∩

Table 2: Summary of regression models separating the effect of elevation on the species richness of the different macrolichen taxonomic-functional groups. As we suspected non-linear relationships between species richness values and elevation, we included elevation also as quadratic term. We omitted the quadratic term if not significant. Significant differences are indicated by bold p-values at $P < 0.05$. The column "direction" indicates either positive, negative, hump-shaped, dip-shaped or non-significant (ns) relationships.

Species richness		Plot			Forest floor			Trees		
		Slope	p	Direction	Slope	p	Direction	Slope	p	Direction
All macrolichens	Intercept	-2.59	0.078		-4.12	0.003		-0.34	0.725	
	Elevation	0.02	<0.001	+	0.01	<0.001	+	0.01	<0.001	+
Green-algae macrolichens	Intercept	-0.71	0.482		-1.57	0.104		0.03	0.961	
	Elevation	0.02	<0.001	+	0.01	<0.001	+	0.01	<0.001	+
Cyano-macrolichens	Intercept	-1.88	0.005		-2.55	<0.001		-0.37	0.496	
	Elevation	0.01	<0.001	+	0.01	<0.001	+	0.01	<0.001	+
Foliose adpressed species	Intercept	-0.65	0.200		-0.33	0.091		0.22	0.259	
	Elevation	0.01	<0.001	+	0.01	<0.001	+	0.01	0.002	+
Foliose ascendant species	Intercept	-0.44	0.588		-0.14	0.485		0.50	0.035	
	Elevation	0.01	<0.001	+	0.01	<0.001	+	0.01	<0.001	+
Fruticose-erect species	Intercept	1.25	0.056		1.26	0.056		0.67	0.054	
	Elevation	-0.01	0.044		-0.01	0.038		-0.01	0.006	
	Elevation ²	0.01	<0.001	∩	-0.01	<0.001	∩	0.01	<0.001	∩
Fruticose-pendulous species	Intercept	-0.74	0.017		-0.14	0.369		-0.29	0.022	
	Elevation	0.01	<0.001	+	0.01	<0.001	+	0.01	<0.001	+

Table 3: Wilcoxon tests showing the effect of disturbances (dist.) on the species richness of different bryophyte and macrolichen functional-taxonomic groups. Significant differences are indicated by bold p-values at $P < 0.05$.

	Plot				Forest floor				Trees			
	no dist.		with dist.		no dist.		with dist.		no dist.		with dist.	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Bryophytes												
All bryophytes	32.1	1.8	25.8	1.4 *	28.1	1.7	21.8	1.3 **	15.0	1.1	12.5	0.8
Liverworts	20.0	1.1	15.2	0.9 **	17.3	1.0	12.5	0.8 ***	11.3	0.8	9.0	0.6
Mosses	12.1	0.9	10.5	0.6	10.8	0.9	9.4	0.6	3.7	0.4	3.5	0.3
Endemics	5.0	0.5	2.6	0.3 ***	3.9	0.5	2.0	0.2 ***	3.1	0.3	1.5	0.2 ***
Red List species	1.1	0.3	0.8	0.1	0.8	0.2	0.6	0.1	0.5	0.2	0.3	0.1
Colonists	7.0	0.5	6.2	0.4	6.6	0.5	5.7	0.4	0.6	0.1	1.0	0.2
Short-lived shuttles	1.4	0.3	0.8	0.1	1.0	0.2	0.7	0.1	0.7	0.2	0.3	0.1
Long-lived shuttles	10.1	0.6	8.5	0.5	8.2	0.6	6.6	0.5 *	7.3	0.5	6.0	0.4
Perennials	13.4	1.0	10.1	0.7 **	12.1	0.9	8.6	0.7 **	6.4	0.6	5.1	0.4
Macrolichens												
All species	11.4	0.9	8.9	1.0 *	8.1	0.9	7.0	0.9 *	5.8	0.5	3.9	0.5 **
Green-algae lichens	7.6	0.6	6.1	0.6 *	6.0	0.6	5.0	0.6 *	3.1	0.3	2.4	0.3
Cyano-lichens	3.9	0.5	2.8	0.4 *	2.1	0.4	2.0	0.4	2.7	0.4	1.5	0.3 **
Foliose adressed sp.	3.0	0.3	2.1	0.3 *	1.9	0.4	1.5	0.3	1.6	0.2	1.0	0.2 **
Foliose ascendant sp.	6.4	0.5	4.2	0.5 **	4.1	0.4	3.2	0.4 *	3.7	0.4	2.0	0.3 ***
Fruticose-erect sp.	0.9	0.2	1.3	0.2	0.9	0.2	1.1	0.2	0.3	0.1	0.5	0.1
Fruticose-pendulous sp.	1.2	0.2	1.2	0.2	1.2	0.2	1.1	0.2	0.2	0.1	0.4	0.1

Figure 1: Location of the 92 plots (black dots) distributed along the elevational gradient from the laurel to the tree-heath forest on Madeira island.

Figure 2: Relationship between the species richness of A) all bryophytes, B) bryophytes on soil, C) bryophytes on trees, D) endemic bryophytes, E) liverworts, F) mosses, G) perennial bryophytes, H) long-lived shuttle species, I) short-lived shuttle species, J) colonist species and elevation (solid line indicates significant relationship). The dashed lines indicate the 95% confidence interval.

Figure 3: Relationship between the species richness of A) all macrolichens, B) green-algae macrolichens, C) cyanobacteria macrolichens, D) fruticose-erect macrolichens and elevation (solid line indicates significant relationship). The dashed lines indicate the 95% confidence interval.

List of appendices

Appendix S1: List of plots with information on date of survey, location (UTM-grid, easting, northing), elevation, type of disturbance and sampled tree species.

Appendix S2: Species list of bryophytes with frequencies and functional-taxonomic group information.

Appendix S3: Species list of macrolichens with frequencies and functional-taxonomic group information.

Appendix S4: Figure showing the effects of disturbances on bryophyte and macrolichen species richness.





