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**Morphological variation in liverworts traits influence  
community assemblage along an elevational gradient in  
northern Madagascar**

 Lovanomenjanahary Marline,  Claudine Ah-Peng,  Olivier Flores,  Terry Hedderson

1 Epiphytic liverworts of the North of Madagascar

2

3 **Morphological variation in liverworts traits influence community assemblage along an**  
4 **elevational gradient in northern Madagascar**

5

6 Lovanomenjanahary Marline<sup>1,2</sup>, Claudine Ah-Peng<sup>3,4</sup>, Olivier Flores<sup>3</sup>, Terry Hedderson<sup>5</sup>

7

8 1. Association Vahatra, Antananarivo, Madagascar

9 2. Royal Botanical Gardens Kew, Antananarivo, Madagascar

10 3. UMR PVBMT, Université de La Réunion, Saint-Pierre, La Réunion, France

11 4. Observatoire des Sciences de l'Université de la Réunion (OSU-Réunion), UAR 3365,

12 Université de la Réunion, CNRS, Météo France, IRD, Saint-Denis, France

13 5. Bolus Herbarium, University of Cape Town, Cape Town, South Africa

14

15 Corresponding author: Lovanomenjanahary Marline, [marlinelova@gmail.com](mailto:marlinelova@gmail.com)

16

17 **Abstract**

18 **Background and aims** – Epiphyte bryophytes play a crucial role in forest ecosystems by  
19 contributing to water retention, nutrient cycling, and microhabitat creation. However, despite  
20 their ecological importance, epiphyte bryophytes in Madagascar remain poorly studied,  
21 especially in terms of their functional traits and responses to environmental change. This study  
22 addresses this gap by investigating epiphytic liverwort communities along an elevational  
23 gradient in northern Madagascar. We aim to assess the relationship between liverwort species'  
24 functional diversity and community assembly using a trait-based approach, focusing on how  
25 habitat filtering and niche differentiation shape community structure.

26 **Material and methods** – Epiphytic bryophytes were collected across 10 elevational belts along  
27 a 2230 m elevational transect. We measured 12 morphological traits related to resource use, life  
28 history, defense, desiccation resistance, and photosynthetic activity. Functional evenness (FEve)  
29 and functional dispersion (FDis) were calculated for each community. To investigate functional  
30 responses underlying community assembly, we measured community-weighted means (CWM)  
31 and variances (CWV) for each trait along the transect. We analyzed trait-environment  
32 relationships using multiple general linear models and evaluated community assembly processes  
33 (convergence or divergence) across the gradient.

34 **Key results** – Community assembly is influenced by environmental conditions and vegetation  
35 structure. At lower elevations, higher temperatures and taller vegetation lead to trait  
36 convergence, particularly in size-related traits. In contrast, at higher elevations, increased species  
37 richness increased trait divergence. Habitat filtering drives trait convergence at lower elevations,  
38 while niche differentiation becomes more important at species-rich higher elevations.

39 **Conclusion** – Morphological traits reveal how habitat filtering and niche differentiation jointly  
40 influence species distribution. Including physiological traits like water-holding capacity and  
41 carbon fixation in future studies will provide deeper insights into ecosystem processes. These  
42 findings contribute to understanding tropical forest ecosystems.

43

44 **Keywords:** Community assembly, elevational gradient, epiphyte liverworts, habitat filtering,  
45 morphological traits, niche differentiation, Madagascar, tropical ecosystems

46

47

## INTRODUCTION

48 Understanding ecosystem function requires quantifying species responses to environmental  
49 changes and the role of biotic interactions in shaping community composition (Gross et al.  
50 2013). Community ecologists increasingly recognize that specific functional traits of  
51 assemblages may significantly influence ecosystem function, often more than species richness or  
52 composition (Hinz et al. 2021, Liu et al. 2021). Consequently, interest in the relationship  
53 between biodiversity and functional diversity has surged in the past decades (Díaz et al. 2007).  
54 Morphological traits, in particular, serve as valuable proxies for understanding functional traits,  
55 as they often correlate with an organism's performance and ecological strategies. These traits can  
56 provide insights into how species interact with their environments and contribute to ecosystem  
57 processes (Cadotte et al. 2011, Wang et al. 2024). Functional diversity encompasses measures of  
58 ecological importance and impacts on ecosystem functions, while also challenging traditional  
59 species assembly rules (Violle et al. 2007). By linking morphological characteristics to  
60 functional traits, we can better understand community assemblage and species contributions to  
61 ecosystem functioning (Davies et al. 2007).

62 Bryophytes, comprising mosses, liverworts and hornworts, are the second most successful group  
63 of land plants after angiosperms in terms of species richness and their geographical distribution.  
64 Bryophytes are poikilohydric (Pardow et al. 2012, Pardow and Lakatos 2013), i.e. their hydration  
65 status depends to a great extent on the water content of their surrounding environment. Many  
66 species have the ability to desiccate completely as the surrounding environment dries out but to  
67 then rapidly resume photosynthesis and growth upon rewetting (Proctor et al. 2007, Pardow and  
68 Lakatos 2013). They lack a root system, absorbing water and nutrients across their surface,  
69 which explains their high sensitivity to air and water pollution (Govindaparyi et al. 2010).  
70 Bryophytes also exhibit functional diversity (e.g. drought tolerance, water retention, etc.)  
71 allowing them to survive in a wide range of climates and habitats, making them suitable  
72 indicators for detecting climate change impacts (Gignac 2001, Bergamini et al. 2009). In tropical  
73 montane systems, they contribute significantly to forest biomass (Pócs 1982, Holz and Gradstein  
74 2005, Gehrig-Downie et al. 2011) and play a crucial role in mist forests due to their high surface  
75 area and water retention capacity (Muchura et al. 2014, Ah-Peng et al. 2017). They often  
76 colonize tree trunks and branches without drawing water or nutrients from living tissues of their  
77 support plants. The overwhelming abundance of epiphytic liverworts in cloud forests is  
78 considered an important factor in mitigating the negative effects of heavy rains, by increasing  
79 slope stability and prevention of soil erosion. Epiphytic liverworts are ubiquitous components of  
80 bryophyte communities in tropical rainforests and provide a classic example of a taxonomically  
81 rich group with varied ecology and life-history (Gradstein and Pócs 1989).

82  
83 This study focuses on epiphytic liverworts collected in the montane rain forest of northern  
84 Madagascar, a region known for its unique biodiversity and complex ecosystems. Despite the  
85 ecological importance of liverworts in forest environments, research on these epiphytes remains  
86 limited, particularly in the context of Madagascar's montane ecosystems. To our knowledge, this  
87 study is the first to investigate the functional traits of epiphytic liverwort communities in this  
88 region, addressing a critical gap in the literature. We investigate the epiphyte liverwort  
89 communities collected along an elevational gradient by assessing the variation of informative  
90 functional traits among species and across elevation ranges on a tropical mountain in the north of  
91 Madagascar. We hypothesize that, if epiphytic bryophyte functional diversity is closely

92 associated with species diversity in rich tropical plant communities, the question is whether more  
 93 functionally similar species can coexist in a confined functional space, or whether there may be a  
 94 greater range of functions involved (Swenson 2011). Moreover, as environmental adversity  
 95 increases toward the upper limits of the elevational profile, especially above the forest line,  
 96 conditions become more extreme, likely promoting trait convergence and reducing functional  
 97 diversity within bryophyte communities. We anticipate more uniformity of traits and decreasing  
 98 functional diversity within communities (Cornwell et al. 2006, Grime 2006, Baldeck et al. 2013).  
 99 Habitat filtering results in a relatively narrower range of trait values occurring in specific  
 100 environmental conditions i.e., species co-existing in communities under habitat filtering usually  
 101 exhibit similarity in life history, morphology, and physiology (Grime 2006). Alternatively,  
 102 competition and the resulting limiting similarity may lead to communities containing dissimilar  
 103 species. Therefore, the co-existence of species in any given community likely results from the  
 104 combined effect of habitat filtering and niche differentiation (Kraft et al. 2009, Jung et al. 2010).

105  
 106 This study addresses the following questions: (1) How do species and functional diversity  
 107 components vary along the elevational gradient? (2) How do traits measured at species and  
 108 community level respond to environmental changes along the gradient? (3) How do bryophyte  
 109 species interact functionally with their abiotic and biotic environments?, and (4) How do habitat  
 110 filtering and niche differentiation influence bryophyte assemblages along the elevational  
 111 gradient?

## 112 MATERIALS AND METHODS

### 113 **Study site**

114 This study was carried out in Marojejy National Park in the SAVA Region of north-eastern  
 115 Madagascar and centered on the Marojejy massif. The mountain's altitude ranges from 250 to  
 116 2132 m, offering a wide elevational gradient that made it an ideal site for examining trait  
 117 filtering across elevations. The rugged topography of the massif creates diverse habitats that  
 118 transition quickly with changes in altitude. The moist evergreen forests occurring in the lower  
 119 elevations gradually transition into montane cloud forest from 1200 m, which is marked by its  
 120 lower canopy and more dense understory, and finally forest line occurs around 1800 m and  
 121 ericoid montane thickets occur to the peak at 2132 m. Rainfall is abundant, and almost no dry  
 122 season has been recorded on the eastern slope of the massif. Across the eastern slope of the  
 123 massif, average annual temperatures range from 14.9°C to 21.8°C, with relative humidity  
 124 consistently high, averaging between 94.8% and 98.9% throughout the year (Marline et al.  
 125 2023).

### 126 **Sampling design and data collection**

127  
 128 Bryophytes were collected along an elevational transect at 200 m intervals along an elevational  
 129 gradient from 250 m to 2050 m and following the hierarchical sampling method described in Ah-  
 130 Peng et al. (2007) and Marline (2018). At each elevational level, two plots measuring 10 x 10 m  
 131 were established. Within each plot, three quadrats of 2 x 2 m were selected randomly. In each  
 132 quadrat, three trees were randomly chosen, and 5 x 10 cm epiphytic bryophyte samples  
 133 (microplots) were collected at three heights: 0-50 cm, 50-100 cm, and 100-200 cm above ground  
 134 level.  
 135  
 136

137 Temperature and relative humidity were monitored using MadgeTech RHTemp1000 data  
 138 loggers, installed at five elevations (450 m, 850 m, 1250 m, 1650 m, and 2050 m) in December  
 139 2013. These loggers recorded temperature and humidity continuously at hourly intervals from  
 140 December 2013 to December 2014. To estimate temperature and relative humidity at locations  
 141 without data loggers, a calibration curve based on elevation was applied. For each elevation,  
 142 vapor pressure deficit (VPD) was calculated as the difference between saturated vapor pressure  
 143 (SVP) and actual vapor pressure (VP) following Monteith and Unsworth (2013). At each  
 144 sampling site canopy height (minimum and maximum) were recorded.

145  
 146 For the species found on the transect we compiled data on 12 morphological traits (Table 1) that  
 147 are likely to be related to resource use, life history, species defense, resistance to desiccation and  
 148 photosynthetic activity, and could be obtained for at least 95% of the collected taxa. Trait values  
 149 for each taxon were collected from the literature or by direct measurements on herbarium  
 150 specimens.

151  
 152

Table 1: Description of 12 morphological traits in liverworts and their ecological function

Traits	Category	Description	Function
Oil bodies	Binary	Unique to liverworts, these are true membrane-bound organelles that contain terpenoid oils suspended in a carbohydrate and/or protein-rich matrix. Ninety percent of liverworts develop them.	They are thought to deter herbivores or provide protection from cold and/or UV radiation (He et al. 2013).
Ocelli	Binary	Unusually large leaf cells that often contain one or more larger-than-usual oil-bodies and lack chloroplasts	Like oil bodies, they are thought to deter herbivores or provide protection from cold and/or UV radiation (He et al. 2013).
Lobule	Binary	Smaller lobes of a complicated-bilobed leaf or a sac formed by an enrolled rear leaf margin (Malcolm and Malcolm 2000).	Lobules have long been interpreted as water-sacs allowing the plant to remain physiologically active when the colonies are subjected to persistent desiccating conditions.
Leaf surface papillae	Binary	A minute, solid protuberance on a cell surface. Developed in some liverwort species	They are thought to increase and maintain water uptake. By creating capillary channels on the leaf surface they appear to aid in retaining water and protecting regions of active cell division from dehydration (Proctor 2008).
Trigones	Binary	Wall thickenings where three adjacent cells meet.	The presence of trigones seems to be a xerophytic adaptation in liverworts (Watson 1914).

Underleaves	Binary	Pseudo-leaves on ventral stem surfaces.	Their presence against the stem could favor the storage of intercepted water through capillarity in order to keep the plant moist and photosynthetically active (Ah-Peng et al. 2017).
Size related traits	Continuous	gametophyte length, gametophyte width, stem diameter, leaf length, leaf width and elongation index (gametophyte length/width ratio).	These traits appear to be related to growth and nutrient retention (Proctor and Tuba 2002).

153

154 **Data analyses**

155 Two multidimensional indices - functional evenness (FEve) and functional dispersion (FDis)  
 156 were used to characterize functional diversity, following the framework proposed by (Botta-  
 157 Dukát 2005, Mason et al. 2005, Villéger et al. 2008, Laliberté et al. 2010). FEve, a measure of  
 158 the evenness of species abundance distributions in functional trait space (Mason et al. 2005,  
 159 Villéger et al. 2008) reflects the degree to which a community can effectively utilize the entire  
 160 range of resources available to it. FDis measures the weighted (by relative abundance) mean  
 161 distance of individual species to their weighted centroid and describes the functional similarity of  
 162 species in a community in trait space. Its variation across species indicates the degree of  
 163 functional redundancy, typically measured across multiple traits, among species within a given  
 164 spatial scale (Laliberté et al. 2010).

165 We used linear regressions to evaluate the relationship between functional diversity indices and  
 166 species richness at elevational scale.

167

168 To investigate potential functional responses underlying the process of community assembly  
 169 along the elevational gradient, we measured the community-weighted means (CWM) and  
 170 community-weighted variances (CWV) for each trait along the elevational transect. The CWM  
 171 for each trait is the mean across species present in the community weighted by their relative  
 172 abundance (Violle et al. 2007, Bernard-Verdier et al. 2012), in this case the frequency of species  
 173 occurrence across smallest sampling units (microhabitat). Similarly,  $CWV_i$ , is calculated  
 174 following (Bernard-Verdier et al. 2012) and (Sonnier et al. 2010). For binary traits,  $CWM_i$   
 175 estimates the total frequency of species sharing the attribute, and  $CWV_i$  estimates the variance in  
 176 this frequency.

177

178 A null model approach was used to test whether the observed trait metrics differ from random  
 179 expectation. Species abundances were randomized across elevations in order to divide existing  
 180 relationships between trait values and species abundance. Random assemblages were constrained  
 181 to observed species richness per elevation. Weighted community traits were computed at each  
 182 iteration, and the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles were obtained from the null distribution to produce  
 183 null confidence intervals across the elevation gradient.

184

185 Comparing the estimated CWM and CWV values to expectations from randomized data allows  
 186 detection of significant functional structuring in observed patterns. Higher values of CWM  
 187 compared to random simulations indicate higher trait values at the community level, or higher  
 188 frequency of species with a given attribute for binary traits. Conversely, values lower than  
 189 expected indicate evidence of ecological filtering towards high or low trait values (Hulshof and  
 190 Swenson 2010, Bernard-Verdier et al. 2012), analogous to directional selection in evolution.  
 191 Compared to random expectations, higher CWV values indicate significantly high variability in  
 192 trait values or, for binary traits, high variability in frequency among species sharing similar  
 193 attributes. Conversely, lower CWV values suggest reduced variability. Such patterns reflect  
 194 ecological convergence/divergence for the considered traits and, indirectly, as evidence of  
 195 competition or ecological filtering (Hulshof and Swenson 2010, Kang et al. 2017).

196  
 197 In order to understand the possible drivers of community functional traits, we build statistical  
 198 models that relate either elevation only, or a combination of elevation and other environmental  
 199 variables to each functional diversity measure and CWM. A multiple general linear model was  
 200 used to select the best multiple combinations of environmental variables associated with  
 201 community functional composition. For the sake of simplicity, we restrict the analyses to metrics  
 202 related to average functional composition (CWM) and not variability (CWV). AIC scores were  
 203 compared for three model types: linear, cubic, and quadratic polynomial, to determine the best  
 204 fit. Models showing significant relationships at the 5% error level were retained. The model with  
 205 the lowest AIC score and highest  $R^2$  value was taken as best explaining the relationship between  
 206 the observed CWM trait values and environmental variables. CWM for binary traits was logit-  
 207 transformed prior to analysis, allowing the consideration of models in a classical Gaussian  
 208 framework for all response variables.

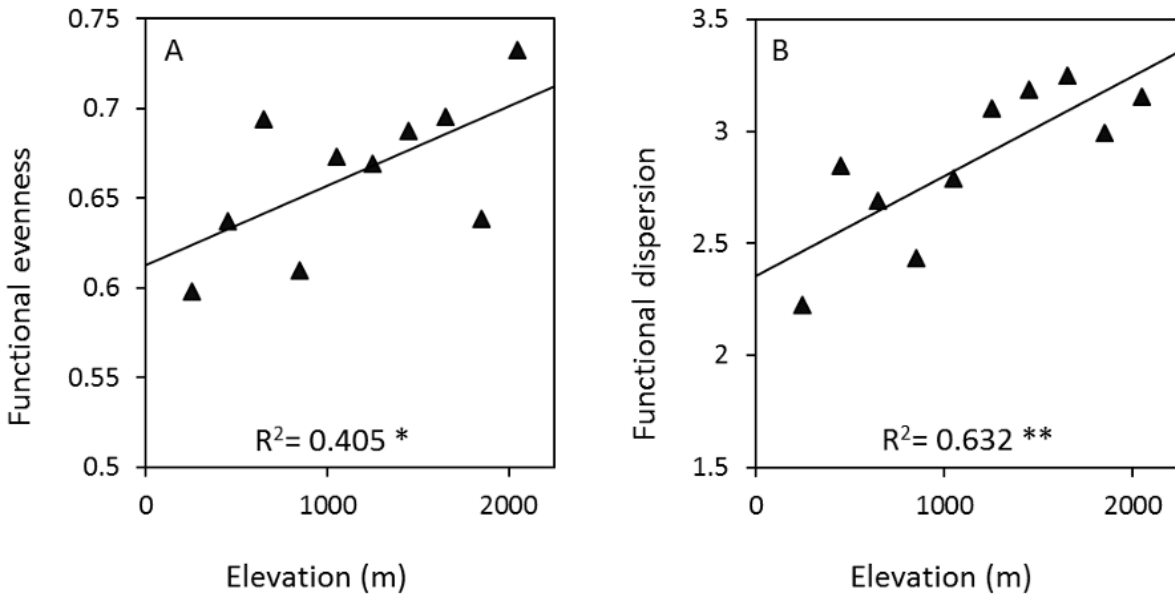
209  
 210 All analyses were conducted with the statistical software R (R Core Team, 2015) and the  
 211 packages Ade4 (Dray 2016), Permute (Simpson 2016), Vegan (Oksanen et al. 2015) and FD  
 212 (Laliberté et al. 2010, 2015).

## 213 214 RESULTS

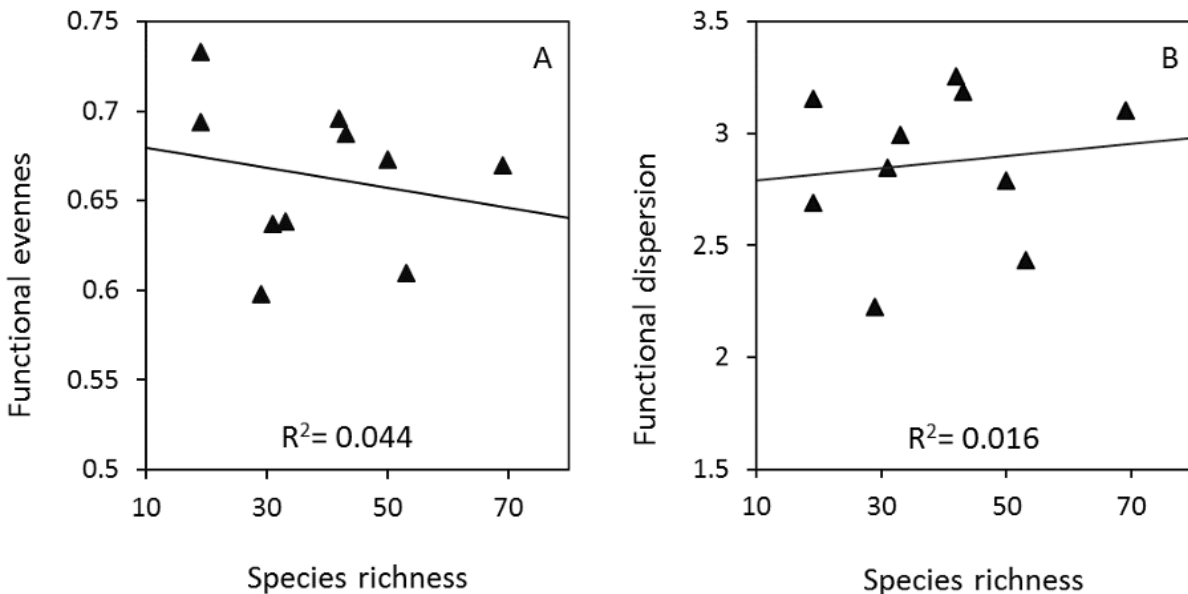
### 215 **Elevational pattern of floristic and functional diversity**

216 The epiphytic leafy liverwort flora of Marojejy National Park comprises 150 species, distributed  
 217 among 44 genera and 18 families. Lejeuneaceae are the most species-rich family and comprise  
 218 nearly half of the total species diversity (73 species in 20 genera). Species richness peaks at 1250  
 219 m (71 species) and lowest species richness was found at 650 m (19 species) and 2150 m (23  
 220 species).

221  
 222 FEve shows an overall significant increase with altitude ( $R^2 = 0.405$ ,  $p < 0.05$ ), as does FDis ( $R^2$   
 223  $= 0.632$ ,  $p < 0.01$ ) (Fig.1A–B). Neither of the two functional diversity indices shows a significant  
 224 relationship with species richness (Fig. 2A–B).



225  
 226 **Figure 1.** Pattern of functional diversity metrics with elevation. A: Functional evenness, B:  
 227 Functional dispersion. R<sup>2</sup> value from a linear regression and 95% confidence level. \* p-value <  
 228 0.05, \*\* p-value < 0.01. Note that vertical axes start above 0.  
 229



230  
 231 **Figure 2.** Linear regression between functional diversities and species richness. A: Functional  
 232 evenness, B: Functional dispersion. R<sup>2</sup> value from a linear regression and 95% confidence level.  
 233

234 **Variation in community means of traits along the elevational gradient**

235 Community weighted means (CWM) for size-related traits (i.e. leaf length, leaf width,  
 236 gametophyte length, gametophyte width, and stem diameter), as well as for papillae and trigone  
 237 presence increase significantly with increasing elevation. CWMs for lobule, ocelli, and oil body  
 238 presence decrease significantly with elevation (Fig. 3, Table 2). CWM for underleaf presence did

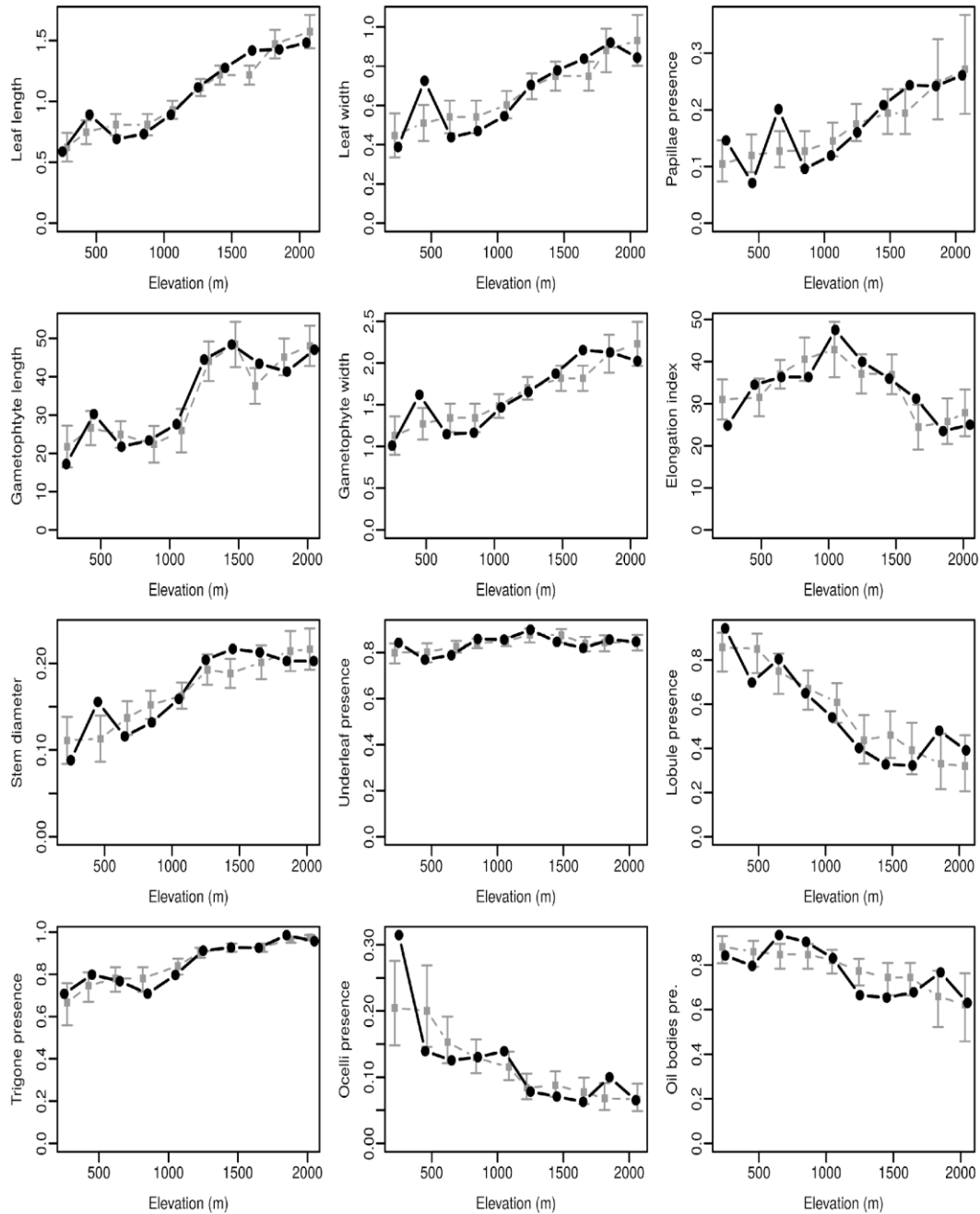
239 not show a significant relationship with elevation. A hump-shaped relationship with elevation  
 240 was found for the elongation index (Fig. 3, Table 2).

241  
 242 **Table 2.** AIC for models of CWM. Cubic elevation models were retained only for papillae and  
 243 trigone presence. Multiple general linear model analysis was performed to select multiple  
 244 combinations of environmental variables that could predict CWM with the lowest Akaike  
 245 Information Criteria (AIC).  $R^2$  is shown for models with climate variables AIClin (linear model),  
 246 AICquad (quadratic polynomial model), and AICcub (cubic model).

Traits	AIClin	AICquad	AICcub	$R^2$	adjusted. $R^2$	Est.	Std. Err.	T	p
Leaf length	-10.95	-9.54	-10.48	0.9	0.89	0.000524	6.38E-05	8.2	***
Leaf width	-11.24	-9.57	-8.57	0.73	0.7	0.000259	6.29E-05	4.12	**
Papillae presence	12.16	13.22	14.05	0.57	0.52	0.000631	0.000203	3.12	*
Gametophyte length	69.11	70.73	71.07	0.92	0.88	0.0166	0.00349	4.74	**
Gametophyte width	1.73	3.61	3.64	0.77	0.74	0.000607	0.00012	5.04	***
Elongation index	73.05	60.66	60.4	0.7	0.61	0.0445	0.0103	4.31	**
Stem diameter	-42.12	-42.5	-42.49	0.75	0.72	6.49E-05	1.34E-05	4.83	**
Underleaf presence	6.12	6.96	8.45	0.5	0.35	0.000167	0.00015	1.11	ns
Lobule presence	23.48	16.24	18.24	0.74	0.7	-0.00511	0.00112	-4.57	**
Trigone presence	19.94	20.62	20.69	0.87	0.85	0.00158	0.000299	5.28	***
Ocelli presence	10.88	8.73	10.08	0.7	0.66	-0.00221	0.000769	-2.88	*
Oil body presence	20.49	22.26	20.41	0.5	0.44	-0.00081	0.000307	-2.64	*

\* p-value < 0.05, \*\* p-value < 0.01, \*\*\*p-value < 0.001, ns not significant

247  
 248 Considering the intraspecific variability did not improve these relationships except for lobule  
 249 presence and trigone presence, where the trigone presence decreases with increasing elevation  
 250 and lobule presence increases with increasing elevation (Fig. 3). The traits showing the strongest  
 251 relationships with environmental variables are leaf length ( $R^2 = 0.9$ ,  $p < 0.001$ ), gametophyte  
 252 length ( $R^2 = 0.92$ ,  $p < 0.001$ ) and trigone presence ( $R^2 = 0.87$ ,  $p < 0.001$ ) (Table 2).  
 253



254  
 255 **Figure 3.** Distribution of community-weighted means (CWM) by elevation (circles) and values  
 256 estimated by linear models from climatic variables (gray). Lines indicate the 95% confidence  
 257 interval for modeled values  
 258

259 **Effect of environmental variables on community trait means**

260 Leaf length, leaf width, gametophyte length, gametophyte width, papillae presence, and trigone  
 261 presence exhibited significant negative correlations with canopy mean height (cmea).  
 262 Conversely, oil body presence showed a significant positive correlation with cmea. Stem  
 263 diameter and underleaf presence were negatively correlated with the mean temperature (temp.m),  
 264 whilst lobule and ocelli presence exhibited significant positive correlation with this variable.

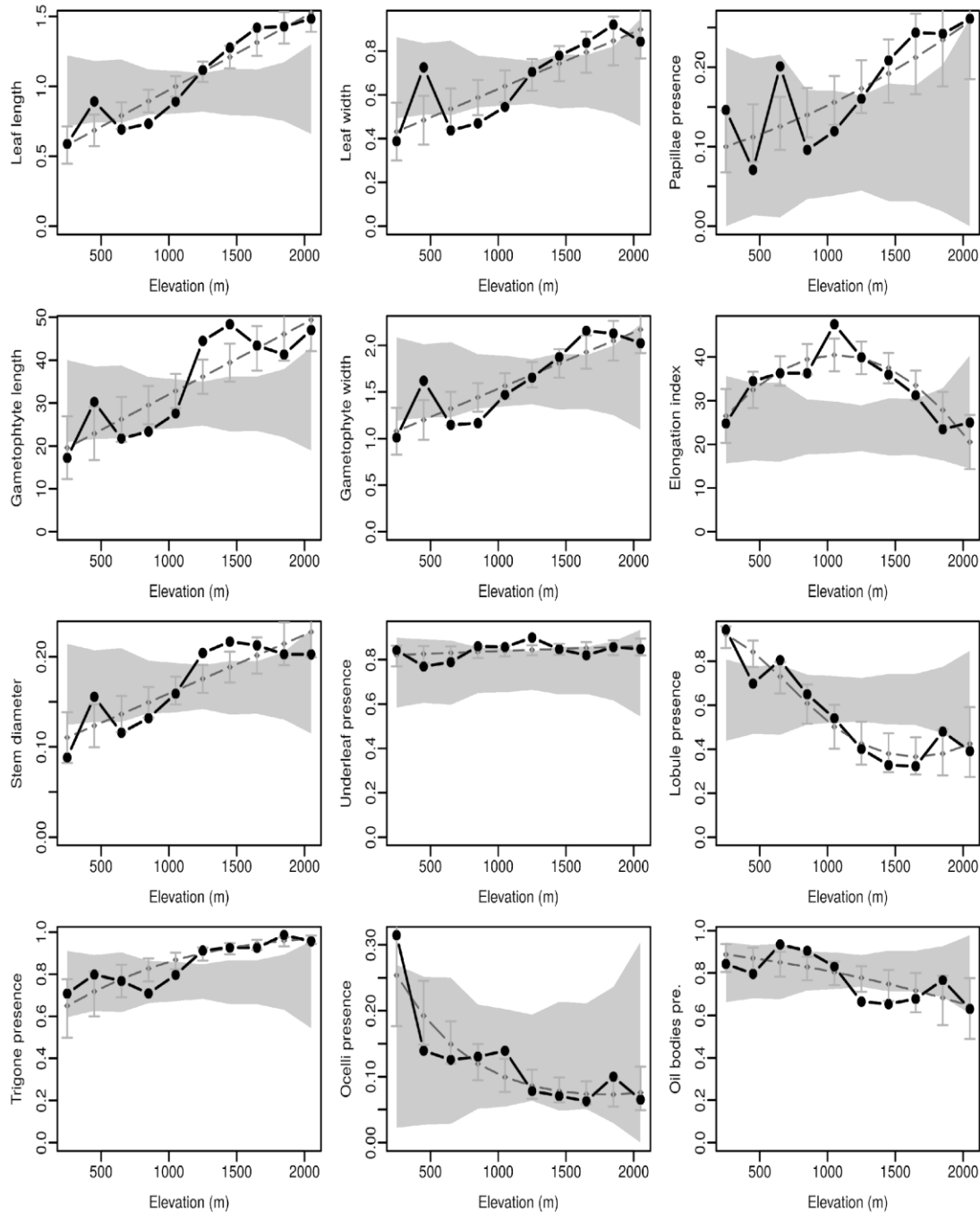
265 Only the elongation index showed a significant correlation with vapor pressure deficit (vpd) and  
 266 a weak correlation with relative humidity (rh.m) (Table 3). This indicates that a high percentage  
 267 of variation in these traits is explained by the corresponding environmental variables.  
 268

269 **Table 3.** Regression coefficients for linear models of CWM with environmental variables. .

Traits		Est.	Std.Err	T	p
Leaf length	cmea	-4.08E-02	0.00471	-8.65	***
Leaf width	cmea	-2.08E-02	0.00446	-4.67	**
Papillae presence	cmea	-4.99E-02	0.01532	-3.26	*
Gametophyte length	cmea	-1.73E+00	0.22753	-7.61	***
	rh.m	1.47E+01	6.07085	2.42	.
	I(vpd <sup>2</sup> )	3.96E-03	0.00187	2.12	.
Gametophyte width	cmea	-4.73E-02	0.00916	-5.16	***
Elongation index	I(vpd <sup>2</sup> )	-5.53E-03	0.00218	-2.54	*
	rh.m	-1.60E+01	7.04997	-2.26	.
Stem diameter	temp.m	-1.69E-02	0.00341	-4.96	**
Underleaf presence	I(temp.m <sup>2</sup> )	-2.46E-03	0.00096	-2.57	*
	I(vpd <sup>2</sup> )	-1.82E-05	1E-05	-1.81	ns
Lobule presence	I(temp.m <sup>2</sup> )	1.07E-02	0.00227	4.72	**
Trigone presence	cmea	-1.29E-01	0.01803	-7.17	***
Ocelli presence	I(temp.m <sup>2</sup> )	5.38E-03	0.00125	4.29	**
Oil body presence	cmea	6.51E-02	0.02307	2.82	***

cmea: mean canopy height, vpd: vapor pressure deficit, temp.m: mean temperature, rh.m: mean relative humidity. (.) p-value < 0.1 \* p-value < 0.05, \*\* p-value < 0.01, \*\*\*p-value < 0.001, ns not significant

270  
 271 **Habitat filtering along the elevational gradient**  
 272 Trait filtering is indicated when means of traits within a community, within an elevational band  
 273 deviate from null expectations. This occurs when certain environmental conditions at a given  
 274 elevation selectively favor species with specific traits, causing the community’s trait composition  
 275 to diverge from what would be expected under random assembly. All traits that we studied, with  
 276 the exception of the presence/absence of underleaf and ocelli, exhibited departures from the null  
 277 model in at least one elevational band (Fig. 4). Filtering for lobule absence is evident at 1250-  
 278 1650 m and oil body presence at 1250-1650 m, and at lower elevation for low values of stem  
 279 diameter (250-850 m) and gametophyte width (250 m, 560-850 m). Observed values of  
 280 community-weighted means (CWM) were higher than expected at higher elevation for leaf  
 281 length (1250-2050 m), leaf width (1650-1850 m), gametophyte length (1250-2050 m),  
 282 gametophyte width (1650-1850m), stem diameter (1250-1650 m), papillae presence (1450-2050  
 283 m) and trigone presence (1250-2050 m). Only the elongation index at mid elevation showed  
 284 significant deviation above the null model.  
 285

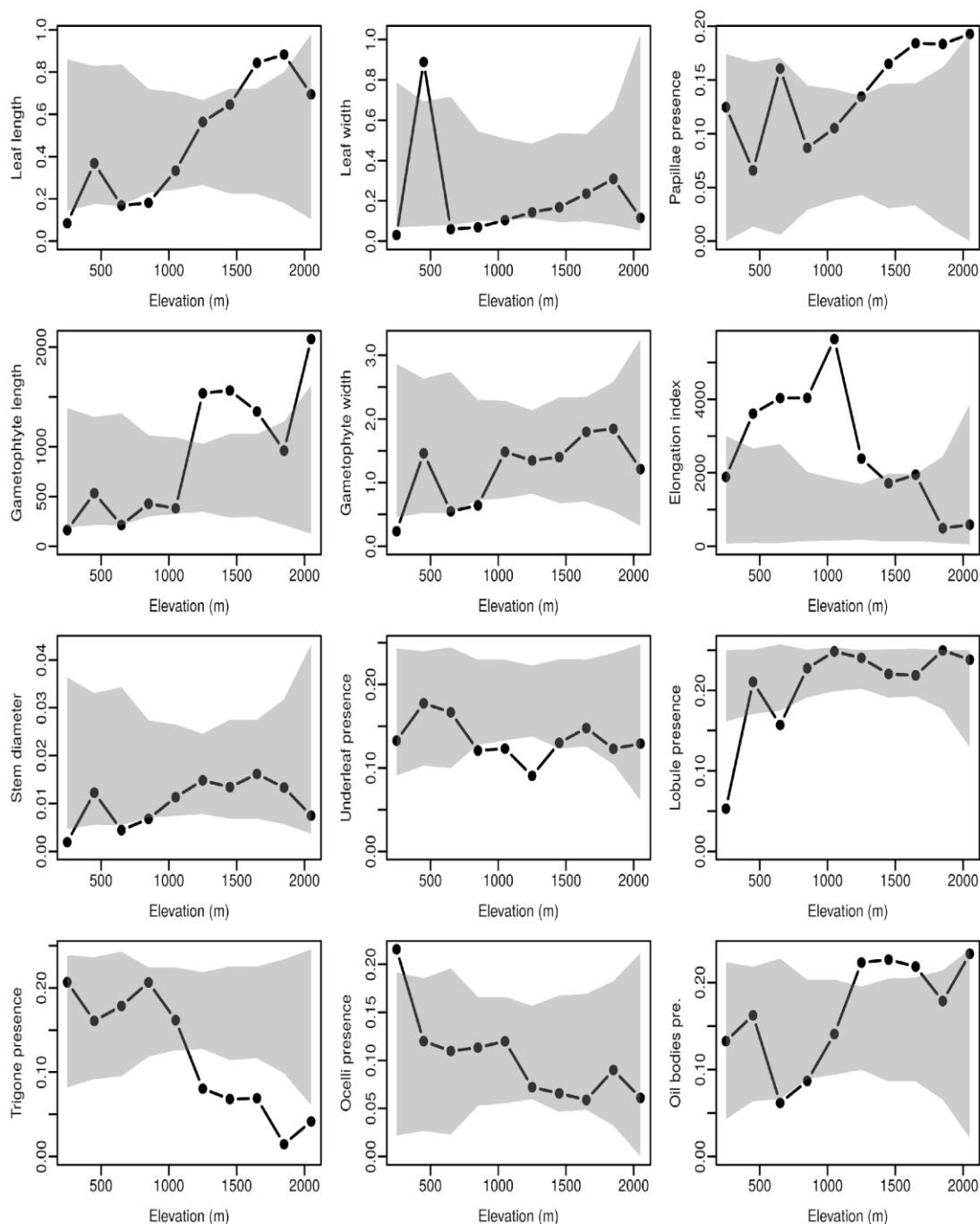


286  
 287 **Figure 4.** Distribution of community-weighted means (CWM) of traits along the elevational  
 288 gradient. Envelope (gray) shows the 95% confidence interval under the null model of random  
 289 community assembly. Squares indicate values estimated by linear models against elevation with  
 290 95% confidence interval.

291  
 292 **Trait divergence along the elevational gradient**

293 Community weighted variances (CWV) for all traits except gametophyte width and stem  
 294 diameter also departed significantly from those expected under a null model at least some  
 295 elevations. Thus, leaf length (1650-1850 m), leaf width (450 m), papillae presence (1420-2050

296 m), elongation index (450-1250 m), gametophyte length (1250-1650 m and 2050 m), ocelli  
 297 presence (250 m), and oil body presence (1250-1650 m) were more variable than expected,  
 298 indicating that those traits have scattered distributions within communities. This means that  
 299 abundant species tend to exhibit dissimilar functional trait values along the elevational gradient.  
 300 By contrast, trait convergence, indicated by lower-than-random CWV values, is detected at 850-  
 301 1250 m for underleaf presence, 1250-2050 m for trigone presence and 250-850 m for lobule  
 302 presence (Fig. 5).  
 303



304

305 **Figure 5.** Distribution of community-weighted variances (CWV) of traits along the elevational  
306 gradient. The envelope (gray) shows the 95% confidence interval under the null model of  
307 random community assembly.

308  
309  
310

## 311 DISCUSSION

312 Patterns and changes in the range and distribution of functional trait values in a community  
313 provide information on spatial and temporal variation in trait diversity, as well as on processes  
314 that drive species assemblages and whether such assemblages are likely to contain redundant  
315 species (Tilman 2001). Neither community-weighted means (CWM) of trait values nor  
316 functional trait diversity metrics have often been incorporated in assessments of ecosystem  
317 services, but to better understand species interaction and community assembly they have recently  
318 been incorporated in biodiversity experiments (Holden and Cahill 2024, Palacio et al. 2024).  
319 The trait-based analyses presented here show that (1) functional evenness and functional  
320 dispersion increase significantly with elevation, (2) the pattern of distribution and variance of  
321 traits within communities along the elevational gradient are dependent on the nature of the  
322 considered traits (3) canopy height and temperature are the most powerful environmental  
323 variables shaping the pattern of CWM distribution, and (4) habitat filtering and niche  
324 differentiation both explained observed species abundance in communities; habitat filtering  
325 (associated with trait convergence) is strongest at lower elevations and niche differentiation  
326 (associated with trait divergence) occurs at higher elevation and is highest at the most species-  
327 rich sites.

328

### 329 **Functional evenness, functional dispersion, and floristic composition**

330 Much attention has been focused on the use of functional traits, and their abundance and  
331 distribution in communities, in the exploration of relationships between biodiversity and  
332 ecosystem functioning (Halpern and Floeter 2008, Cadotte et al. 2009, Mouillot et al. 2011,  
333 Roscher et al. 2012, Correia and Lopes 2023). The positive relationship between functional  
334 evenness and elevation found here suggests a more regular functional distance among species as  
335 elevation increases (Villéger et al., 2008). The fact that more individuals of the common species  
336 are recorded as elevation increases suggests liverwort functional traits are not evenly distributed  
337 along the elevational gradient. Functional dispersion quantifies the extent of functional similarity  
338 among species in the trait space. The increase in functional dispersion with elevation indicates  
339 low redundancy in the liverwort community. This is consistent with the idea that new species  
340 added at each elevation are less similar than the existing species and reflects dissimilar functional  
341 traits across abundant species (Karadimou et al. 2015, Ferrara et al. 2024).

342

### 343 **Trait variation at different ecological scales**

344 A main goal of this work was to determine which environmental factor(s) influence the variation  
345 and distribution of CWM of liverworts traits across the elevational gradient. This study suggests  
346 that canopy height and temperature are the most powerful environmental variables shaping the  
347 pattern of trait distributions. Relative humidity and vapor pressure deficit, on the other hand,  
348 have a weaker effect on trait variation and distribution among communities.

349

350 The leafy liverwort communities showed a clear functional response along the elevational  
 351 gradient, as demonstrated by the observed clear pattern in community-weighted means for nine  
 352 of the 12 traits (Fig. 3). The abundance-distribution of all traits related to plant size significantly  
 353 increased with elevation, indicating that at high elevation there is more variation in plant size  
 354 (Henriques et al. 2017). Papillae and trigone presence are thought to be related to water retention  
 355 and xerophytic adaptation respectively. Papillae may facilitate water uptake by creating capillary  
 356 spaces (Proctor 1979), whilst elongated cells with trigones enhance water uptake from the  
 357 surrounding environment (Vitt et al. 2014). This study shows that the abundance of species with  
 358 those traits also increases significantly with elevation, potentially as a response to the rougher  
 359 environmental conditions at elevations higher than 1800 m. Lobules are often referred to as  
 360 water sacs and, like papillae and trigones, an increasing CWM for lobule presence would have  
 361 been expected. However, its CWMs were negatively related to increasing elevation. Since the  
 362 lobules are characteristics of most species of the Lejeuneaceae, this pattern can be related to the  
 363 fact that the Lejeuneaceae are most abundant at lower and mid-elevations. A similar result was  
 364 found for ocelli presence, although the functional role of this feature is yet to be elucidated.

365

### 366 **Habitat filtering and niche differentiation**

367 Both habitat filtering and niche differentiation appear to be involved in structuring species  
 368 abundances in the communities studied here. Our results add to the growing body of evidence for  
 369 the joint effect of these two processes on community structure (Cornwell and Ackerly 2009, Jung  
 370 et al. 2010, Mason et al. 2011, Maire et al. 2012).

371

372 In the system studied herein, trait filtering appears to occur toward both ends of the elevational  
 373 gradient. This is in line with (Mayfield and Levine 2010) hypothesis on the occurrence of  
 374 ecological filtering at the extremities of environmental gradients. According to (Bernard-Verdier  
 375 et al. 2012), this is due to the differential filtering of dissimilar traits along a gradient. The  
 376 detection of ecological filtering is critically dependent on the studied trait. Different traits,  
 377 related to various functional roles, exhibited filtering at different parts of the elevational gradient.  
 378 At low elevation, where diversity is lower, the range of traits directly linked to growth and  
 379 nutrient acquisition (gametophyte and leaf size) exhibits filtering (Herben and Goldberg 2014).  
 380 This can be related to competition for light, given the fact that at low elevations in a tropical  
 381 forest the canopy is continuous, and the canopy height is the highest. This may account for the  
 382 abundance of small and narrow species. At low elevations, for instance, the most abundant  
 383 species include: *Bazzania nitida* (F. Weber) Grolle, *Ceratolejeunea stictophylla* Herzog ex  
 384 Vanden Berghen, *Cololejeunea appressa* (A. Evans) Benedix, *Heteroscyphus dubius* (Gottsche)  
 385 Schiffn., *Lejeunea confusa* E.W. Jones, and *Prionolejeunea grata* (Gottsche) Schiffn..  
 386 None of the studied traits, except for lobule and oil body presence, were specifically filtered at  
 387 mid-elevation, suggesting that these provide the most favorable habitats for epiphytic liverworts.  
 388 Interestingly, at mid-elevation trait variation is either randomly distributed or divergent  
 389 (elongation index only) due perhaps to the relaxation of environmental constraints allowing for  
 390 the coexistence of a wide range of functional strategies and therefore a peak of diversity at the  
 391 center of a gradient. Trait range reduction detected at mid-elevation suggests that trait filtering  
 392 may also occur in more stable habitats (Bernard-Verdier et al. 2012).

393

394 Towards higher elevations, leaf length, leaf width, and gametophyte length tend to be divergent  
 395 in communities. This suggests that traits related to plant size coexist successfully, and species are

396 less similar to each other (Funk et al. 2008). This trend can be explained by the wide range in  
397 size exhibited by the most abundant species. Tall liverwort species such as *Herbertus dicranus*  
398 (Taylor ex Gottsche et al.) Trevis and *Mastigophora diclados* (Brid. ex F. Weber) Nees are about  
399 as abundant as small species such as *Conoscyphus trapezioides* (Sande Lac.) Schiffn. and  
400 *Drepanolejeunea physaefolia* (Gottsche) Steph. at higher elevations.

401  
402 The divergence in leaf length, leaf width, gametophyte length, papillae presence, elongation  
403 index, and oil body presence provide strong evidence of niche differentiation, although  
404 mechanisms such as limiting similarity or facilitation cannot be inferred here.

#### 405 406 CONCLUSION

407 This study provides evidence that assemblage of the epiphytic liverwort community on a massif  
408 in the north is driven by climatic conditions and vegetation structure, affecting the occurrence of  
409 species among and within communities. It demonstrates that traits tend to shift from convergent  
410 to divergent with an increasing elevation. Higher temperature and taller vegetation appear to  
411 have driven a strong functional convergence of size-related traits (except for leaf width) at lower  
412 elevations but have allowed for divergence in these at higher elevations.

413  
414 This is the first study to investigate bryophyte functional trait variation along an elevational  
415 gradient in Madagascar. Only morphological traits potentially related to resource use, life  
416 history, species defense, resistance to desiccation, and photosynthetic activity were studied.  
417 However, other physiological traits related to features such as photosynthetic capacity and  
418 carbon fixation, superimposed on phylogenetic relatedness, need to be considered for further  
419 study and for a better understanding of the relationship between species composition and  
420 ecosystem processes in this ecologically important but grossly understudied plant group.

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