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Original Article

Morphoanatomical functional traits of terrestrial acrocarpous mosses in *campos de altitude*

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ABSTRACT

The high-altitude fields (in Portuguese, *campos de altitude*) of the Itatiaia National Park (INP) hold the greatest moss endemism and number of threatened species known to Brazil. We examined the morphoanatomical functional traits of acrocarpous mosses along a post-fire disturbance gradient in the *campos de altitude* of the INP, verified the existence of functional groups, and evaluated the functional compositions of their assemblies. To that end, we elaborated a matrix of the morphoanatomical characters of the mosses, compiled a total of 24 functional traits related to drought and/or light tolerance from the literature, and subsequently applied multivariate techniques to analyze the data. The mosses displayed functional traits that allowed them to survive under the environmental conditions imposed in *campos de altitude*. Their main traits were related to leaf curvature, coloration, and costa width. The functional compositions of those communities were different along the different successional stages, with changes in species compositions and functional groups being associated with phylogenetic patterns.

Keywords: Atlantic Forest, bryophytes, high-altitude grasslands, functional traits, post-fire succession

Introduction

Campos de altitude ("high-altitude fields") are ecosystems within the Atlantic Forest phytogeographic domain. They occur above the tree line near the highest mountain peaks in southeastern Brazil (Safford, 1999a). The solar radiation levels in those fields, as well as temperature and humidity conditions, vary widely during the year (Safford, 1999b), and the plants that grow there retain strategies that allow them to either tolerate or avoid high-stress conditions (Safford, 1999a; Ribeiro *et al.*, 2007).

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The small areas occupied by high-altitude fields, as well as their isolation, make them especially vulnerable to anthropic threats such as habitat loss and wildfires. Additionally, indirect human influences, such as climate change, are expected to expose those ecosystems to increasingly extended dry periods in the coming decades, principally during the winter months (Martinelli, 2007; Aximoff, 2011; Scarano *et al.*, 2016; Gonçalves *et al.*, 2023).

The Itatiaia National Park (INP) is regarded as one of the principal centers of bryophyte diversity and endemism in the neotropical region (Gradstein *et al.*, 2001; Gradstein & Costa, 2003; Costa & Faria, 2008; Gonçalves & Santos, 2018). The high-altitude fields (in Portuguese, *campos de altitude*) vegetation at INP, where much of that bryophyte diversity is found, is subject to many environmental disturbances, including both natural and anthropogenic wildfires. Those disturbances can impact plant community structures and favor the arrival and dominance of invasive species (Aximoff & Rodrigues, 2011; Tomzhinski *et al.*, 2012). Wienskoski & Santos (2022) studied the bryophytes occurring along post-fire gradients in the INP and reported different species compositions in different areas. Significant environmental and micro-climatic alterations occur in burnt areas, including sudden increases in incident solar radiation resulting from the elimination of vegetation cover. Additionally, the soils become more alkaline due to the incorporation of plant ashes (Ryömä & Laaka-Lindberg, 2005; Thomas *et al.*, 1994), and support substrates (such as decomposing tree trunks and branches) essential to many species, become scarce, leading to the prevalence of bryophytes growing only on open ground and rock surfaces (Wienskoski & Santos, 2022).

Bryophytes are currently regarded as a monophyletic group composed of three phyla: Anthocerotophyta, Bryophyta, and Marchantiophyta (Puttick *et al.*, 2018; One Thousand Plant Transcriptome Initiative, 2019; Harris *et al.*, 2020; Li *et al.*, 2020; Donoghue *et al.*, 2021). Mosses are included within the phylum Bryophyta, currently considered a sister group to the Marchantiophyta, forming the Setaphyta clade (Puttick *et al.*, 2018; Li *et al.*, 2020), which is characterized by the presence of seta connecting the sporangia to the base of the sporophyte. Mosses form the most structurally diverse phylum among the bryophytes (Goffinet & Shaw, 2009) and demonstrate the greatest taxonomic richness in environments with high incident light levels, such as savannas (Carmo & Peralta, 2016), rock outcrops (Silva *et al.*, 2014), and *campos de altitude* (Wienskoski & Santos, 2022). Acrocarpous mosses predominate on *campos de altitude* soils (Wienskoski & Santos, 2022), where they produce apical gametangia and usually demonstrate vertical (orthotropic) growth (Mägdefrau, 1982; La Farge-England, 1996). We will consider here only species demonstrating orthotropic growth, which, because of the historic association between the terms acrocarpous and orthotropic, will be referred to hereafter simply as acrocarpous mosses. Acrocarpous growth becomes a relevant factor for the occurrence of mosses in environments such as *campos de altitude*, as they form turfs or cushions – life forms usually associated with less humid environments exposed to high solar radiation levels having high tolerance to stress and disturbance conditions (Birse, 1957; Mägdefrau, 1982; Bates, 1998; Schmitz *et al.*, 2018). Although these mosses produce relatively small biomasses compared to other plants commonly found in *campos de altitude*, they play important roles there as pioneer species on soil islands on rocky outcrops (Ribeiro *et al.*, 2007; Silva *et al.*, 2020), or in areas that have experienced environmental disturbances (such as the passage of fire) (Duncan & Dalton, 1982). The ecological ability of pioneer species is related to a series of physiological and morphoanatomical functional traits that provide these plants with tolerance to high light intensity and desiccation (Proctor *et al.*, 2007; Glime, 2017a; b).

Characteristics that allow plants to occupy different environments and pass different environmental filters must possess appropriate functional characters (Rosado *et al.*, 2013). Organisms that demonstrate functional traits that allow similar responses to similar environmental filters can be considered to form functional groups (de Bello *et al.*, 2010; Díaz & Cabido, 2001). It is worth stressing that a given attribute can demonstrate more than one functionality in a plant, and different traits can lead to the same performance or display the same function (Silva *et al.*, 2018; Dias *et al.*, 2020). Among the anatomical traits of acrocarpous mosses important for water uptake are internal tissues (hydrome and leptome) that conduct water and/or metabolites (Glime, 2017a). To prevent or reduce water losses, mosses frequently produce leaves with specialized structures such as hyalocysts (cells that store water) that facilitate leaf margin folding as the plants become dry; those leaves can likewise have papillose surfaces and/or plicated zones that increase the surface area available for gas exchange and the space available for water conduction through capillarity (Watson, 1914; Schofield, 1981; Glime, 2017c). Many mosses also produce recurved leaves that spiral around the stem, thus facilitating water adhesion and capillary transport (Glime, 2017c).

Even with this basic knowledge of the structures and mechanisms important to the ecology and survival of bryophytes, the relative importance of each in the ecological success of any given species requires a detailed examination (Schofield, 1981; Glime, 2017b). As such, the present work was designed: (i) to investigate the morphoanatomical functional traits of acrocarpous mosses in *campos de altitude* in the INP; (ii) to determine if those same traits define functional groups among those mosses; and, (iii) to evaluate the functional compositions of moss assemblies located in areas demonstrating distinct post-fire successional stages.

We hypothesized that: (i) species can be grouped in different strategies represented by their functional traits, and (ii) distinct strategies will be related to the post-fire successional gradient. In that respect, assemblages in areas that have experienced recent fires would be expected to demonstrate characteristics that maximize protection against solar radiation (*e.g.*, dark pigmentation and papillae) and facilitate the accumulation of water resources (*e.g.*, hyalocysts).

Material and methods

Study area

The Itatiaia National Park covers approximately 280 km^2 within four municipalities of two Brazilian states: Itatiaia and Resende in Rio de Janeiro State, and Bocaina de Minas and Itamonte in Minas Gerais State (22°22’10.9” S, 44°37’42.6” W). The *campos de altitude* of the INP are located above the tree line, between 1800 and 2200 m above sea level (Safford, 1999a), and are subject to a high-altitude tropical climate, with a mean annual temperature of 11.5° C, and mean annual rainfall levels between 1000 and 2500 mm (Segadas-Vianna & Dau, 1965). The mean annual temperature there in 2020 was 10º C, the total annual precipitation was 2237 mm, while the maximum solar radiation level in 2018 was above 4000 KJ/m^2 (Tabela de Dados das Estações, 2021). The regional rainy season normally extends from December through February and the dry season from June to August. Those climatic conditions, allied to the pedological and geomorphological characteristics of the region, limit arboreal vegetation in most *campos de altitude* areas, making grasses the predominant vegetation form (Segadas-Vianna & Dau, 1965). The INP has a long history of wildfires. The most extensive and longest fire seasons were recorded for the years 1963 (10,000 ha burned), 2001 (600 ha), 2004 (600 ha), 2007 (800 ha), and 2010 (1,100 ha) (Aximoff & Rodrigues, 2011; Aximoff, 2011). Additionally, there was a controlled burn for fire suppression training within the park in 2017.

Data generation and analysis

A dataset of 24 morpho-anatomical characters of the acrocarpous mosses was compiled from the literature (Tab. 1) and elaborated to better record the character states of the functional traits of those species (Tab. 2). The species list utilized here was based on the plants inventoried as occurring in the PNI and identified by Wienskoski & Santos (2022), whose sampling was undertaken in three areas located along a post-fire chronosequence (areas that had been burned in the years 2017, 2007, and 2001) as well as in two control areas in the *campos de altitude* of the INP (Fig. 1). In each area, three transects measuring 20 x 1m were randomly defined in the margin of trails (areas 2001, 2017 and control trail) or roads (areas 2007 and control road). The control areas ("control trail": located along a trail to "Morro do Couto" and "control road": between the "Posto do Marcão" and "Abrigo Rebouças" localities) have not experienced recent fires and present vegetation typical of *campos de altitude*.

The functional traits dataset was composed of the structural data of the gametophytes (the dominant phase in the life cycles of those mosses) gathered from the specialized taxonomic literature, as well as through the analysis of material collected by Wienskoski and Santos (2022). It is worth noting that we included the mamillose and prorulous states in the papillose state.

Multivariate ordination techniques were used to verify the existence of functional groups among the species analyzed. To that end, the data of the functional dataset (with species being considered samples, and the morpho-anatomical traits being considered descriptors) were converted to binary data or to semi-quantitative categories (Tab. 1). That matrix was submitted to Nonlinear Principal Components Analysis (for categorical data – CatPCA) via the 'princals' function of the *gifi* package (Gifi, 1990) in the R platform environment (R Core Team, 2020).

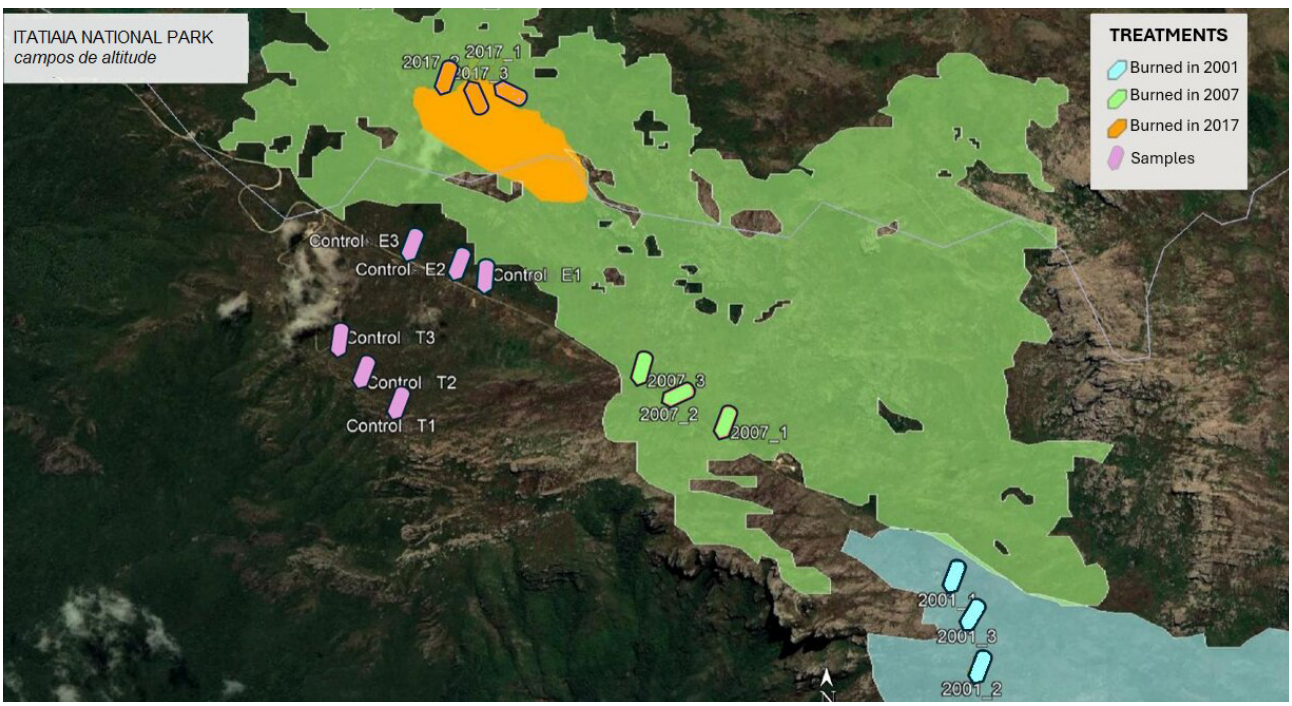

Figure 1. Map of the study areas in *campos de altitude* in the Itatiaia National Park, RJ, Brazil. Locations of the transects: fire 2017 – Cinco Lagos Trail; fire 2007 – between Posto do Marcão and Abrigo Rebouças; fire 2001 – Prateleiras Trail; control trail (T) - Couto Trail; control road (E) – between Posto do Marcão and Abrigo Rebouças. Modified from: Wienskoski (2019).

The Community-weighted means (CWM) of each trait attribute of the acrocarpous moss assemblages present in each area along the post-fire gradient were calculated via the *FD* package in the R platform (Laliberté & Legendre, 2010; Laliberté *et al.*, 2014; R Core Team, 2020). The CWM index calculates the average of trait values weighted by the relative abundance of each species in the community (Garnier *et al.*, 2004), and it is used in functional ecology to summarize shifts in mean trait values due to environmental filtering (Ricotta & Moretti, 2011). The following matrices were used in those analyses: (i) the functional matrix; and, (ii) the floristic matrix, which consisted of bryophyte frequency data (their occurrence along the transects) in the areas inventoried by

Wienskoski & Santos (2022) along the post-fire chronosequence. That matrix did not consider eight species of *Campylopus* (due to the high number of unidentified morphotypes) nor rare species (those that occurred in only a single transect, *i.e.*, singletons). A PCA was used to evaluate the relationship between the CWM and the disturbance gradient, via the *FactoMineR* and *Factoextra* packages (Husson *et al.*, 2007) in the R program (R Core Team, 2020). All of the graphic representations were edited and/or generated using Fitopac software (Shepherd, 2010).

Results

Functional traits

Twenty-four morpho-anatomical traits of the 31 acrocarpous moss species recorded in the INP *campos de altitude* were evaluated (Tab. 2), with seven characteristics treated as binary and 17 as semi-quantitative categories (Tabs. 1 and 2). Of the total 24 traits analyzed, seven were related to solar radiation, 11 to water resources, and six to both light and water factors. Their probable functionalities are described in Table 3.

Table 1. Categories adopted to describe the functional traits of the acrocarpous mosses found in the campos de altitude of the Itatiaia National Park, Brazil. The abbreviations are described in Table 3.

Functional attribute	0	1	2	3	4	5
Ext	Absent	Present				
L_apx	Without tip/obtuse	Rhombic	Sharp	Acuminate	Apiculate	Piliferous
H_ap	Absent	Present				
L_pap	Absent	Present				
Col	Light green, whitish	green, yellowish	Reddish - dark brown	Blackish		
L_st	Absent	Present				
Cen_c	Absent	Present				
L_cur	Recurved/reflexed	Planar	Undulate or plicate	Curved	Falcate	Concave
L_arr	Distich/planar	Rosette	Spiraled			
L_pos	Evident to squarrose	Expanded/erect	Imbricate	Adpressed		
V_ep	Hyalocyst	Substereids	Stereids	Lamella		
D_ep	Hyalocyst	Ribbed/substereids	Stereids	Lamella		
W_cst	Smaller or equal to half of the lamina	Equal to half of the lamina	Stereids greater or equal to half of the lamina			
Cst	Subcurrent	Percurrent	Excurrent			
Tuft	Absent	Present				
Tmt	Absent	Present				
BL_col	Green	Red, brown or dark brown	Blackish or hyaline			
UL_col	Green	Red, brown or dark brown	Blackish or hyaline			
B_cell	Isodiametric; squarish; short hexagonal	Oval; rectangular; rhomboid; long hexagonal	Vermicular; linear			
M_cell	Isodiametric; squarrose; short hexagonal	Oval; rectangular; rhomboid; long hexagonal	Vermicular; linear			
U_cell	Isodiametric; squarrose; short hexagonal	Oval; rectangular; rhomboid; long hexagonal	Vermicular; linear			
C_mar	Abaxial	Planar	Adaxial			
S_mar	Smooth	Serrulate;denticulate	Serrate; dentate			

Table 2. Matrix of the functional traits of acrocarpous mosses in campos de altitude in the Itatiaia National Park, Brazil. Abbreviations described in Table 3.

Species	Abbreviations	Ext	L_apx	H_ap	L_pap	Col	L_st	Cen_c	L_cur	L_arr	L_pos	V_ep	D_ep	W_cst	Cst	Tuft	Tmt	BL_col	UL_col	B_cell	M_cell	U_cell	D_mar	C_mar	S_mar
Anomobryum julaceum (Schrad. ex P. Gaertn. *et al.*) Schimp.	Ano_jul	0	0	0	0	1	1	1	4	2	2	2	0	1	1	0	1	2	0	1	1	2	0	1	1
Barbula indica (Hook.) Spreng	Barb_ind	0	2	0	2	1	1	1	1	2	1	1	0	1	1	0	0	1	1	1	0	0	0	1	0
Breutelia grandis (Hampe) Paris	Bre_gra	0	4	0	1	1	1	1	2	2	0	2	0	1	2	0	1	0	0	1	1	2	0	0	1
Bryum arachnoideum Müll. Hal.	Bry_ara	0	5	1	0	1	1	1	2	2	2	2	0	1	2	0	0	1	0	1	1	1	0	1	0
Bryum argenteum Hedw.	Bry_arg	0	4	1	0	0	1	1	2	2	2	0	0	1	1	0	0	1	0	1	1	1	0	1	0
Bryum billardieri (Schwägr.) J.R. Spence	Bry_bil	0	4	0	0	1	1	1	2	1	2	0	0	1	2	1	0	1	1	1	1	1	1	1	2
Bryum capillare (Hedw.) J.R. Spence	Bry_cap	0	4	0	0	2	1	1	0	1	2	0	0	1	2	1	0	1	1	1	1	1	1	1	1
Bryum subapiculatum Hampe	Bry_sub	0	4	1	0	1	1	1	1	2	2	2	0	1	2	0	0	1	1	1	0	1	0	1	1
Campylopus arctocarpus (Hornsch.) Mitt.	Cam_arct	0	3	0	0	1	1	1	3	2	2	0	1	2	1	0	1	1	2	1	1	1	0	2	1
Campylopus carolinae Grout	Cam_car	0	5	1	0	2	1	1	3	2	3	0	1	3	1	0	1	1	2	1	1	1	1	2	0
Campylopus fragilis (Brid.) Bruch & Schimp.	Cam_fra	0	3	0	0	1	1	1	3	2	2	0	1	3	1	1	1	1	1	1	1	0	0	2	1
Campylopus heterostachys (Hampe) A.Jaeger	Cam_het	0	3	0	0	1	1	1	3	2	2	0	1	3	2	0	1	1	1	1	1	1	0	2	1
Campylopus julicaulis Broth.	Cam_jul	0	3	0	0	2	1	1	3	2	3	0	1	3	2	0	1	1	1	1	1	0	1	2	0
Campylopus lamellinervis (Müll.Hal.) Mitt.	Cam_lam_lam	1	3	0	0	1	1	1	3	2	2	0	2	2	1	0	1	1	1	1	1	0	1	2	1
Campylopus lamellatus Mont	Cam_pil	1	3	1	0	1	1	1	3	2	2	0	2	3	1	0	1	1	1	1	1	1	0	2	1
Campylopus savannarum (Müll.Hal.) Mitt.	Cam_sav	0	3	1	0	1	1	1	1	2	2	0	1	2	1	0	1	1	1	1	1	1	1	2	1
Ceratodon purpureus var. stenocarpus Bruch & Schimp.	Cer_pur	0	3	0	0	2	1	1	1	2	1	0	0	1	1	0	0	1	2	2	2	1	0	0	1
Chrysoblastella chilensis (Mont.) Reimers	Chr_chi	1	3	0	2	1	1	1	1	2	1	2	0	1	2	0	0	0	1	1	1	0	0	1	1
Cladastomum ulei Müll. Hal.	Cla_ule	0	3	0	0	1	1	1	5	2	3	1	0	1	0	0	0	1	1	1	0	0	0	2	1
Fissidens anguste-limbatus Mitt.	Fis_ang	1	4	0	0	3	1	0	1	0	2	0	2	1	2	0	0	3	3	1	0	0	1	1	2
Itatiella ulei (Broth. ex Müll. Hal.) G.L.Sm.	Ita_ule	1	2	0	1	3	1	1	3	2	3	0	2	3	2	0	0	1	1	1	0	0	0	2	2
Leptodontium araucarieti (Müll.Hal.) Paris	Lep_ara	0	2	0	2	1	1	0	3	2	1	2	0	3	0	0	0	0	0	1	1	1	0	0	2
Leptodontium stellatifolium (Hampe) Broth.	Lep_ste	0	2	0	2	2	1	0	3	2	0	2	0	3	0	0	0	2	0	1	1	0	0	0	0
Philonotis hastata (Duby) Wijk & Margad.	Phi_has	0	3	0	1	1	1	0	3	2	1	2	0	1	0	0	1	0	0	1	1	1	1	2	2
Plagiomnium rhynchophorum (Hook.) T.J.Kop.	Pla_rhy	0	0	0	0	1	1	1	2	0	0	0	0	1	1	0	1	1	1	1	0	1	1	1	0
Pohlia camptotrachela (Renauld & Cardot) Broth.	Poh_cam	0	3	0	0	1	0	1	1	2	2	1	1	1	0	0	0	1	1	2	1	1	0	1	0
Pohlia elongata Hedw.	Poh_elo	0	3	0	0	1	0	1	1	2	2	1	1	1	0	1	0	1	1	1	1	1	0	1	2
Pohlia papillosa (Müll.Hal. ex A.Jaeger) Broth.	Poh_pap	0	3	0	0	1	0	1	1	2	2	1	1	1	0	1	0	1	1	2	1	1	0	1	0
Polytrichum angustifolium Mitt.	Pol_ang	1	3	0	1	2	1	1	3	2	3	3	2	2	2	0	0	2	2	1	0	0	0	2	2
Polytrichum commune L. ex Hedw.	Pol_com	1	3	0	0	2	1	1	3	2	3	3	2	3	2	0	0	2	2	1	0	0	0	2	2
Polytrichum juniperinum Willd. ex Hedw.	Pol_jun	1	4	0	0	2	1	1	3	2	3	3	2	3	2	0	0	2	2	1	0	0	0	2	2

Table 3. Descriptions of the morpho-anatomical traits of acrocarpous mosses in the campos de altitude of the Itatiaia National Park, Brazil. The colors denote traits related to light (orange), water (blue), and light and water (green).

Abbreviation	Description	Function	Mechanism	References
Ext	Leaf - presence of a lamina extension (lamellae or vaginant lamina)	Extension of photosynthetically active periods in dry environments	Leaf chlorophyll concentrated in a region in which humidity is preserved for more time; provides a greater area for CO2 absorption	Frahm (1985); Glime (2017b); Kurschner (2004); Proctor (2005)
L_apx	Leaf - apex shape	Protection against high solar radiation levels and excessive UV radiation	Reflects part of the incident solar radiation	Spence (2012); Glime (2017b)
H_ap	Leaf - presence of hyaline apex	Protection against high solar radiation levels and excessive UV radiation	When dry, the leaves of many mosses assume a position adpressed to the stem, so that the upper portions of the leaf laminas and/or their piliferous apex overlap the basal photosynthetic region of the more apical leaves, protecting them from cell damage.	Glime (2017b)
L_pap	Leaf - presence of papillae	Protection against high solar radiation levels and excessive UV radiation; water conduction	Reflect or absorb part of the incident solar radiation. Provides passive spaces that can be filled with water through capillarity.	Glime (2017b)
Col	Gen. color of the plant	Protection against high solar radiation levels and excessive UV radiation	Filtering the light spectrum, principally the highest energy photons, reducing damage to the cytoplasmic material	Glime (2017b)
L_st	Leaf - presence of stereids	Water conduction; structural support against loss of cell turgor due to water losses.	Water transport via the apoplast, through thick and elongated hydrophilic cell walls	Glime (2017b)
Cen_c	Central strand - stem	Water conduction	Water transport through the interior and/or walls of specialized elongated cells (hydroids and/or stereids)	
L_cur	Leaf - curvature	Water conduction; water storage	Provides passive spaces that can be filled with water through capillarity	Glime (2017b)
L_arr	Leaves - placement along the stem	Water conduction; water storage; minimizes the effects of high solar radiation and excessive UV radiation	Provides passive spaces that can be filled with water through capillarity; reduces the area of solar radiation incidence.	Glime (2017b)
L_pos	Leaf - position (angle to the stem)	Minimizes the effects of high solar radiation and excessive UV radiation	Reduces the area of solar radiation incidence; Provides passive spaces that can be filled with water through capillarity.	Glime (2017b)
V_ep	Leaf – types of cells of the ventral epidermis of the costa	Water conduction; water storage; minimizes the effects of high solar radiation and excessive UV radiation	Reduces the area of solar radiation incidence, promoting the closing or rolling up of the leaves when dry through the loss of turgor	Glime (2017b)
D_ep	Leaf - types of cells of the ventral epidermis of the costa	Water conduction; water storage; minimizes the effects of high solar radiation and excessive UV radiation	Reduces the area of solar radiation incidence, promoting the closing or rolling up of the leaves when dry through the loss of turgor	Glime (2017b)
W_cst	Leaf - width of the costa (in relation to the width of the leaf)	Water conduction and storage; structural support against loss of cell turgor due to water losses; photosynthesis with reduced water losses	Greatest concentration of photosynthetic activity in a structure thicker than the lamina and often surrounded by stereids, which can reduce water losses to the environment	Glime (2017b)
Cst	Leaf - length of the costa in relation to the lamina	Water conduction and storage; structural support against loss of cell turgor due to water losses; protection against high solar radiation and excessive UV radiation	Excurrent costa frequently form a piliferous apex, often hyaline, that reflect light and that, when overlapping the photosynthetic bases of the of the leaves when adpressed to the stem under drought situations, can reduce the amount of incident solar radiation and possibly create a more humid microenvironment that would reduce water losses through evaporation	Glime (2017b)

Table 3. Cont.

Abbreviation	Description	Function	Mechanism	References
Tuft	Leaves grouped at the plant apex	Protection against high solar radiation and excessive UV radiation; water storage	Shading by light reflection or absorption; provides passive spaces that can be filled with water through capillarity.	Glime (2017e)
Tmt	Presence of a covering of rhizoids on the stem	Water conduction, water storage; protection against high solar radiation and excessive UV radiation	Provides passive spaces that can be filled with water through capillarity	Glime (2017b)
BL_col	Leaf - pigmentation in the basal region	Protection against high solar radiation and excessive UV radiation	Filtering the light spectrum, principally the highest energy photons, reducing damage to the cytoplasmic material	Glime (2017b)
UL_col	Leaf - pigmentation in the apical region	Protection against high solar radiation and excessive UV radiation	Filtering the light spectrum, principally the highest energy photons, reducing damage to the cytoplasmic material	Glime (2017b)
B_cell	Leaf - shape of the cells in the basal region of the lamina	Water conduction, water storage	Osmosis and/or diffusion	Glime (2017b)
M_cell	Leaf - shape of the cells in the median region of the lamina	Water conduction, water storage	Osmosis and/or diffusion	Glime (2017b)
U_cell	Leaf - cell shapes in the apical region of the lamina	Water conduction, water storage	Osmosis and/or diffusion	Glime (2017b)
D_mar	Leaf - presence of a differentiated margin	Water conduction	Osmosis and/or diffusion	Glime (2017b)
C_mar	Leaf - curvature of the margins	Water conduction, water storage	Provides passive spaces that can be filled with water through capillarity	Glime (2017b)
S_mar	Leaf - shapes of the margins, edges	Uncertain	Uncertain	Glime (2017c)

Functional groups

The diagrams obtained from CatPCA (Figs. 2-3) explained 18.6% of the observed variation along axis 1; 16.4% of that along axis 2; and 13.1% of that along axis 3. The traits that demonstrated the greatest correlation with the first axis were: the curvature of the lamina (correlation = -0.81), type of cell of the ventral epidermis of the costa (-0.78), curvature of the leaf margins (-0.76), width of the costa (-0.73), and the positions of the leaves on the stem (-0.72) (Table S1). The traits most correlated with the second axis were: the color of the basal lamina of the leaves (-0.71), the general color of the plant (0.66), the shape of the leaf apex (0,64), and leaf arrangement (-0.62). The traits most correlated with the third axis were: the presence of tomentum (-0.69) and the presence of hyaline hairpoints (-0.62).

In general, the species were grouped by family along axes 1, 2, and 3 of the CatPCA (Figs. 2-3). The species of Polytrichaceae grouped to the left of the diagram (Figs. 2-3) are characterized by the placement of their imbricated and adpressed leaves, and by the presence of stereids and lamellae. The genus *Pohlia* (family Mniaceae) formed a grouping characterized by leaves composed of elongated (rectangular) cells (Figs. 2-3). The species of Bryaceae were characterized principally by having leaves with apex acuminate to apiculate, mostly hyaline, and elongated (rectangular) cells in their median/superior regions (Figs. 2-3). The species of *Campylopus* (Leucobryaceae) formed an isolated group in the lower left-hand quadrant (Fig. 3), especially due to having leaves with a wide costa of the excurrent type, and curved margins, stereids, and tomentum. The latter character (tomentum) also united a group of species from other families, such as *Philonotis* (Bartramiaceae), *Anomobryum julaceum* (Bryaceae), and *Cladastomum ulei* (Ditrichaceae), as can be seen in the PCA (Fig. 2). Finally, Pottiaceae species stood out principally by the presence of papillose leaves with serrated margins, although they formed neither a cohesive nor isolated group (see axis 3 – Fig. 3).

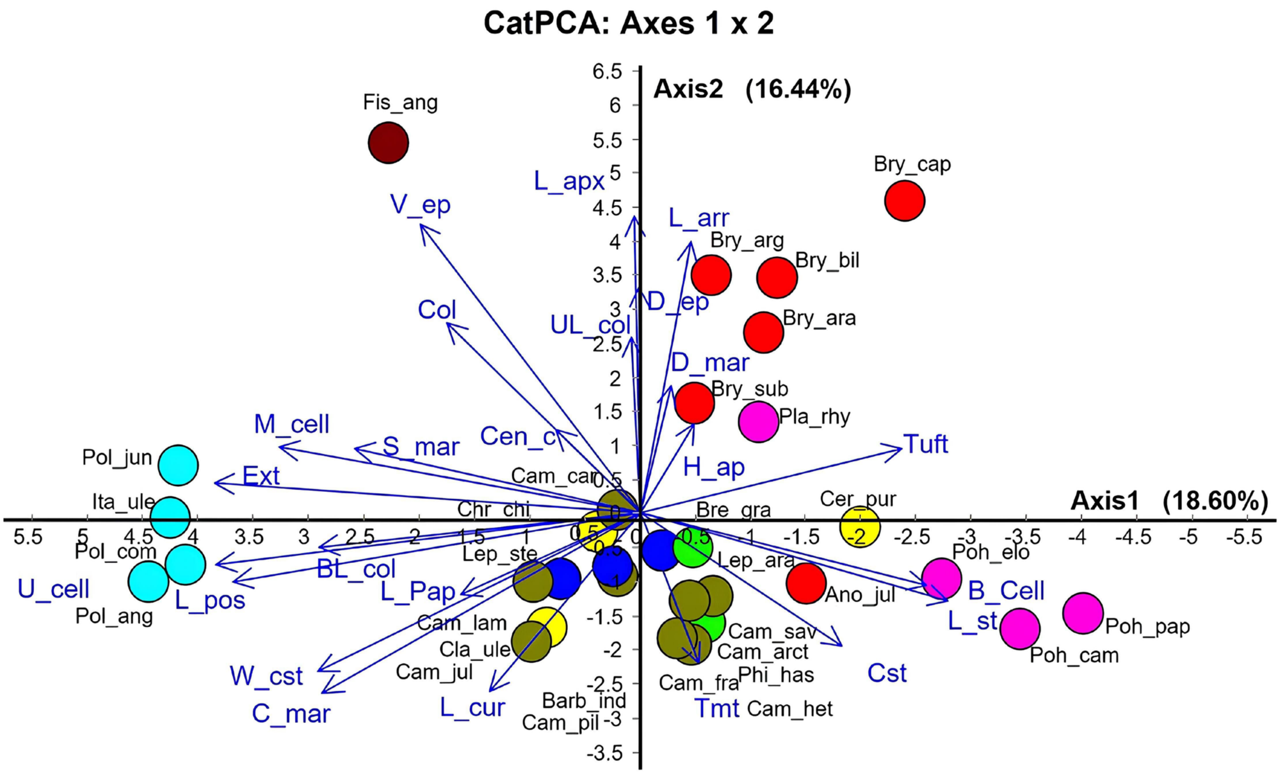

Figure 2. Biplot diagram of the ordination (axes 1 and 2) of the Principal Components Analysis of the functional matrix of the acrocarpous mosses present in the *campos de altitude* of the Itatiaia National Park, Brazil. The different colors denote different families. The full species names are available in Table 2, and their functional traits in Table 3.

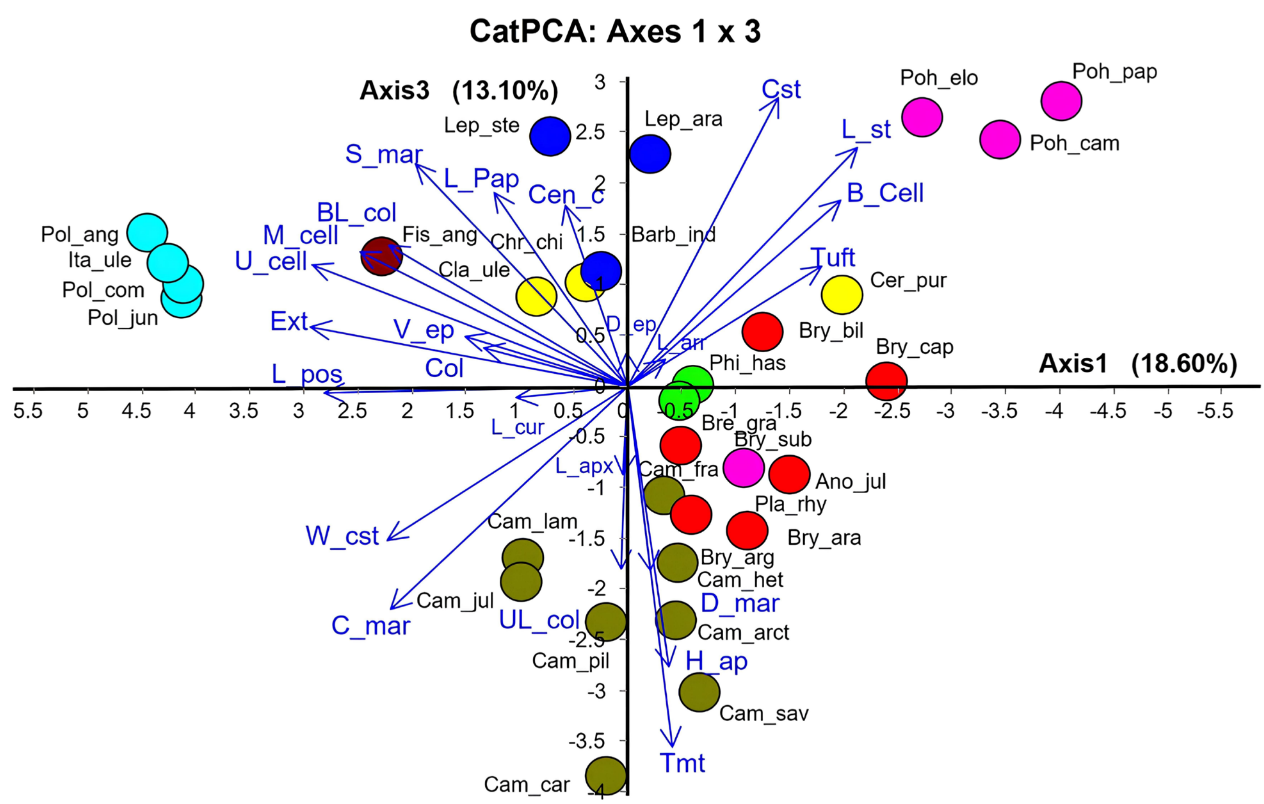

Figure 3. Biplot diagram of the ordination (axes 1 and 2) of the Principal Components Analysis of the functional matrix of the acrocarpous mosses present in the *campos de altitude* of the Itatiaia National Park, Brazil. The different colors denote different families. The full species names are available in Table 2, and their functional traits in Table 3.

Functional compositions of the areas

The biplot of the PCA diagram with the CWM data explained 79.15% of the variations of axes 1 and 2 (Fig. 4). The traits that demonstrated the greatest correlation with the first axis were related to the leaf, being: apex (correlation -0.99), shapes of the cells in the median portion of the lamina (-0.99), leaf margin curvature (0.99), leaf curvature (0.98), and the shape of the cells in the basal portion of the lamina (-0.98). The traits most correlated with the second axis were: plant color (0.94), type of costa (-0.9), and shapes of the cells of the upper portion of the lamina (-0.84).

The area burned in 2001 appeared separate from the other areas along the first axis, being characterized by the presence of plants with leaves with an obtuse apex, adaxial concavity, and irregular margins (serrulate, denticulate, or dentate). It is also important to note that very few families were represented in that area, making it distinct from the others (Fig. 4). The "control trail" area was observed to be separate from the other areas along axis 2 and was characterized as containing an assemblage of mosses having more reddish to blackish coloration. It should be noted that Polytrichaceae predominated in later successional areas (controls and 2001). The areas that experienced burning in 2007, 2017, and the "control road" area formed a less cohesive group located between the mid-region and the lower left quadrant of the biplot and were represented by plants with leaves having an acute to acuminate apex, hyaline, and with planar and entire margins. Of those, two areas (2007 and 2017) also demonstrated greater percentages of species of the family Bryaceae, while the family Bartramiaceae was well-represented only in area 2017.

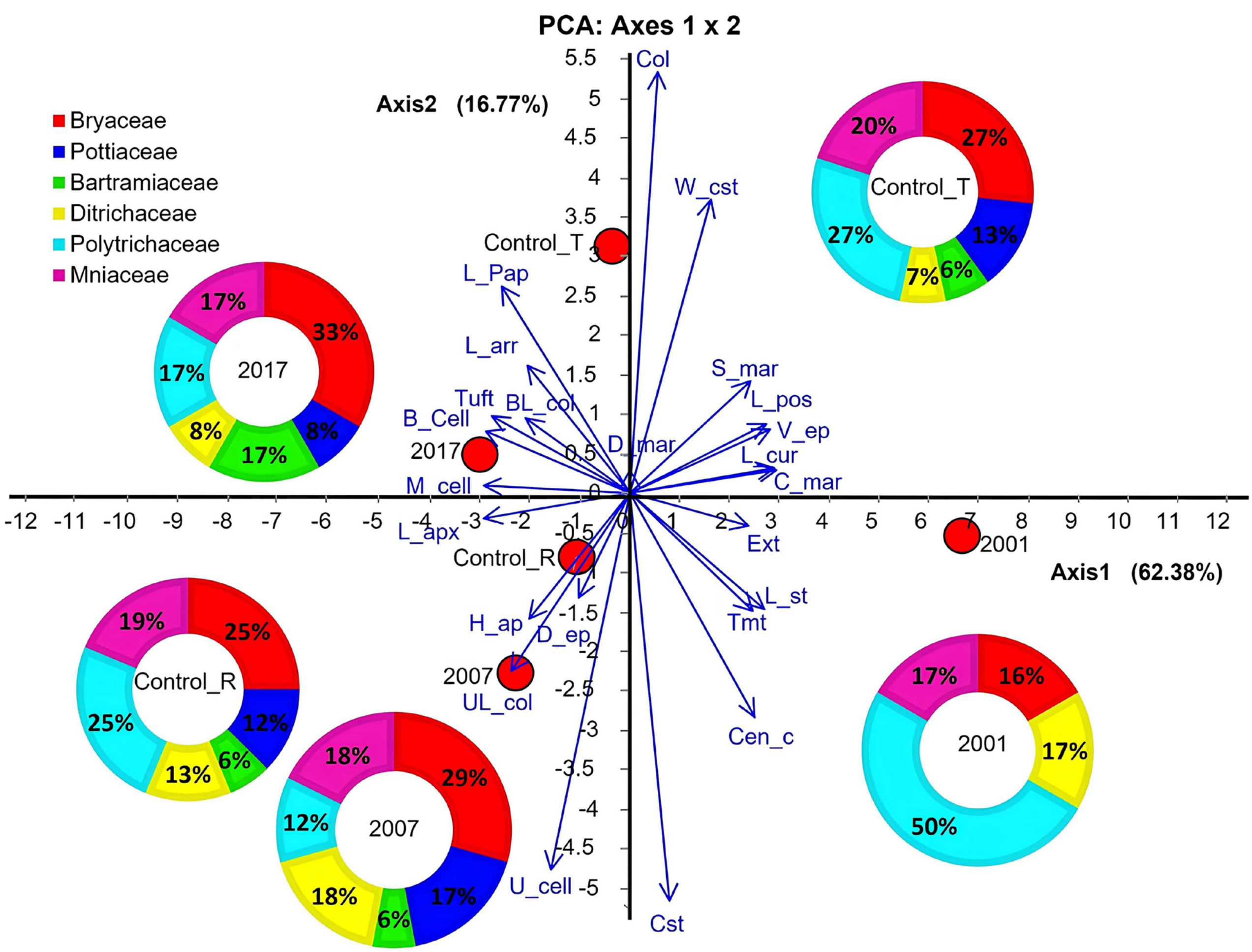

Figure 4. Biplot diagram of the ordination (axes 1 and 2) of the Principal Components Analysis of the CWM values calculated for the chronosequence analyzed in the *campos de altitude* of the Itatiaia National Park, Brazil. The descriptions of the functional traits are available in Table 3. The donut-shaped graphs show the representability of moss families in the assemblages of each site.

Discussion

1) Functional traits of mosses in campos de altitude

As hypothesized, we identified diverse functional traits among the acrocarpous mosses studied that allow them to tolerate the adverse environmental conditions of *campos de altitude*. Among these traits is the presence of hyalocysts in the ventral epidermis of the costa of *Campylopus*. According to Frahm (1985), those structures are related to water capture and storage. The author observed that species with well-developed ventral hyalocysts are generally found in microhabitats with constantly available water. In contrast, species with smaller hyalocysts or with stereids (thick-walled elongated cells with a narrow lumen) on the ventral epidermis, are associated with environments more susceptible to dry periods or subject to greater variations in microenvironmental conditions (such as those encountered in recently burned areas) (Frahm, 1985). The prevalence of small hyalocysts or stereids reflects the necessity of having resistant epidermal cells that do not collapse during desiccation events (Frahm, 1985).

Lamellae were observed principally in representatives of the genera *Campylopus* (Leucobryaceae) and *Polytrichum* (Polytrichaceae). Frahm (1985) reported that those structures in *Campylopus* tended to be present (or more developed) in species associated with dry environments, and suggested that lamellae had a role in extending periods of photosynthetic activity in dry environments by concentrating the leaf chlorophyll in spatially protected regions where humidity could be preserved for longer periods (and even longer when the leaf lamina wrap around the lamellae area). That observation corroborates the data presented by Glime (2017b) and Kürschner (2004) for mosses found in desert environments, as well as the results published by Proctor (2005) for Polytrichaceae. The latter author also suggested that, by providing greater surface areas for gas exchange, the lamellae would allow greater CO_2 absorption, which would then cease to be a limiting factor for photosynthesis; that trait would also allow these mosses to take advantage of low incident light levels. In high-altitude environments, where the UV index of solar radiation is extreme (Alexandris *et al.*, 1999), mosses with lamellae would have a competitive advantage in terms of incorporating atmospheric CO_2. Kürschner (2004) also suggested that lamellae have roles in external water transport by capillarity.

In terms of traits related to incident sunlight, the presence of high concentrations of photo-protective pigments in mosses, such as xanthophylls, phenylpropanoids, flavonoids, and carotenoids can confer resilience and/or resistance to the deleterious effects of high exposures to UVB radiation, including damage to genetic material and the photosynthetic apparatus (Post, 1990; Jorgensen, 1994; Lovelock & Robinson, 2002; Robinson & Waterman, 2014). These photo-protective pigments can be found in the cell interior, or even in the cell walls (Clarke & Robinson, 2008). Some of the species encountered in this study area, such as *Bryum capillare* and *Leptodontium stelatifolium,* have yellowish or brownish colorations due to the presence of photo-protective pigments; *Fissidens anguste-limbatus* and *Itatiella ulei* demonstrated dark brown to blackish tones, suggesting that they may be especially tolerant to high UV irradiation. The presence of photo-protective pigments as one of the characters that best represented the assemblage of the "control trail" area, as can be seen in Fig. 4, reflects the intense insolation in *campos de altitude*.

The presence of a piliferous apex and/or hyaline regions on the leaf lamina can likewise provide advantages to moss species growing in areas exposed to high solar radiation levels (Frey & Kürschner, 1991; Kürschner, 2004; Glime, 2017a). Hyaline cells can reflect significant amounts of incident light, and they lend a silvery color to leaves, whether along the lamina or at the leaf apex. Extensive hyaline regions were observed on mosses growing in *campos de altitude* in the INP, including *Anomobryum julaceus, Bryum arachnoideum,* and *B. argenteum;* the leaves of *Bryum arachnoideum, B. argenteum, B. subapiculatum, Campylopus carolinae, C. pilifer,* and *C. savannarum* had acute to acuminate apices. The leaves of most mosses assume adpressed positions on the stem when they become dehydrated, with the upper portions of the leaf lamina and/or the piliferous apex overlaying the basal photosynthetic regions of the more apical leaves – thus helping to reduce water loss and UV damage in the latter (Proctor, 1979 *apud* Glime, 2017d; Glime, 2017b, c, d). The areas in which this character was more representative were the area burned in 2007 and the "control road" area, thus hinting at a possible greater exposition to the sun.

Another adaptive feature of some of the mosses studied here are the papillae. These structures increase leaf surface reflectivity when the leaves are dry but allow light passage when the leaves are moist (Glime, unpublished data, *apud* Glime, 2017a). The papillae-bearing mosses observed in the present work were *Barbula indica, Breutelia grandis, Chrysoblastella chilensis, Itatiella ulei, Leptodontium araucarieti, L. stelatifolium, Philonotis hastata,* and *Polytrichum angustifolium.*

In terms of internal water conduction, almost all of the mosses analyzed here had stems with central strands – a common attribute of acrocarpous mosses. Central strands can be composed of hydroids and/or stereids, which conduct water more rapidly through the body of the plant than by diffusion through the parenchyma. Leptoids also occur in the central strands of the stems of Polytrichaceae species, but are responsible for metabolite transport (Ligrone *et al.*, 2000).

Silva *et al.* (2018) pointed out that some bryophyte traits demonstrate more than one functionality for the plant. Papillae, for example, can provide a certain level of opacity to the leaves, while at the same time creating capillary spaces for water capture and conduction.

2) Functional groups of acrocarpous mosses

The morphoanatomical traits analyzed here allowed the definition of distinct functional groups demonstrating, in general, phylogenetic patterns, *i.e.*, species of the same families demonstrated similar traits since many of the morphoanatomical characters recorded are evolutionarily highly conserved within higher taxa and have been used for taxonomic classification. The groups identified here present distinct strategies for responding to the environmental filters of *campos de altitude* (*e.g.*, high solar radiation and wide moisture variations). The group formed by species of the genus *Polytrichum* (Polytrichaceae) that also included *Fissidens* (Fissidentaceae, with low similarity), is characterized by the presence of extended leaf lamina, whether in the form of a vaginant lamina in *Fissidens* or as lamellae in Polytrichaceae. A vaginant lamina represents an extra lamina located near the basal portion of the leaf; it is found exclusively in the genus *Fissidens* (Bordin & Yano, 2013) and constitutes an important strategy for water retention. The presence of lamellae (structures that concentrate photosynthetic activities) can be advantageous for mosses that must tolerate drought periods of greater or lesser intensity and frequency, as those structures allow water conservation for longer periods (Kürschner, 2004; Proctor, 2005; Glime, 2017c). Lamellae were also present in some of the *Campylopus* species studied here, although on the dorsal surface of the costae, unlike the lamellae of Polytricaceae. Regarding *Fissidens*, it presents a distichous arrangement of the leaves, something not shared by any other species in the present study.

The genus *Campylopus* (Leucobryaceae), represented by species both with and without lamellae, formed a cohesive group in CatPCA. The most influential traits in the grouping of *Campylopus* (Leucobryaceae) were the presence of concave leaves with curved margins, stereids, and a wide costa, excurrent. This wide costa can favor water absorption by the plant when its ventral epidermis is composed of hyalocysts (Frahm, 1985), as observed in the species of *Campylopus* examined here. Hyalocysts may facilitate water transport between the leaf and stem, similar to the more internal stereids (which also provide structural support) (Frahm, 1985). Additionally, the presence of superficial stereids in the costae can aid photosynthetic activity by reducing water losses to the environment (Frahm, 1985). The concave shape of the leaves and their curved margins may likewise favor the capture and retention of rainwater, and aid in its transport through capillarity (Frahm, 1985).

The Bryaceae were observed to be tightly grouped and were characterized by having leaves with elongated and hyaline apices (L_apx; UL_col; H_ap). Both characteristics increase leaf reflectivity and may help protect the entire plant, including its photosynthetic regions, from excessive solar radiation (Frey & Kürschner, 1991; Kürschner, 2004; Glime, 2017b).

The Mniaceae, likewise, formed a reasonably tight group comprising the three species of *Pohlia* considered in the present work. This group was characterized principally by having elongated cells in the basal and central regions of their leaves. The shapes of those cells may be related to mechanisms for leaf opening and closing, as well as to the internal conduction of water, although there have been no studies directly examining those functions (Glime, 2017c).

The presence of papillae in leaves (L_pap) and serrate or dentate leaf margins (S_mar) were the principal traits grouping the three species of Pottiaceae. Papillae can aid in the capture and conduction of water by capillarity (Proctor, 1979; Longton, 1988), and may also increase the reflectivity of dry leaves – which would constitute a mechanism to reduce UV radiation damage (Glime, unpublished data, *apud* Glime, 2017b). Photo-protective mechanisms (whether structural like these or pigment-based) would be expected to be important to mosses growing in polar regions (Post, 1990; Clarke & Robinson, 2008), at high elevations (Glime, 2017b), or in the *campos de altitude* of INP where UV radiation levels are high (Safford, 1999b). In terms of the shapes of bryophyte leaf margins, their possible functional advantages continue to be topics of debate (Glime, 2017c).

3) Functional compositions along the post-fire gradient

The area burned in 2001 differed from the others by having a predominance of mosses whose leaves were curved to concave, with apices tending to be obtuse and its cells isodiametric, with an extended lamina (principally in the form of lamellae) and stems with a central strand. Curved to concave leaves may be related to water capture and retention, while lamellae can improve photosynthetic production with some UV protection, characteristics associated with dry and/or open, relatively exposed, environments. Still, the presence of leaves with isodiametric cells and obtuse apexes does not relate to very dry conditions (Frahm, 1985; Glime, 2017c). Those general characteristics in combination seem to indicate the occupation of an environment exposed to changing conditions, subject to high luminosity and dry conditions, but also subject to occasional water abundance (Frahm, 1985; Glime, 2017c). Those conditions are similar to the highly variable atmospheric conditions typical of the *campos de altitude* and may point to a relatively exposed microenvironment (Safford, 1999a; b). As was mentioned earlier, the morphological aspects of the mosses demonstrate phylogenetic patterns. As such, the distinct functional composition of area 2001 reflects its species composition, which includes only some of the families present in the other areas (Polytrichaceae, Ditrichaceae, Mniaceae, and Bryaceae). Polytrichaceae, which comprise 50% of the species found in the 2001 area, demonstrates the principal traits encountered there (leaves with extended lamina, isodiametric cells, and leaf apices that tend towards obtuse). Polytrichaceae species have the largest and most robust gametophytes, with the greatest internal water transport efficiencies, and generally colonize sunny roadside slopes and mountaintops (Peralta & Yano, 2010). It is important to note that after the 2001 fire, the burned area was exceptionally colonized by non-clumping grass species, differing from the usual clumping grasses that predominate in the Itatiaia *campos de altitude* (Sylvestre LS, personal obs. 2021). The growth of those grasses may have diminished the availability of microhabitats essential to many species of acrocarpous mosses (*e.g.*, humid and shaded sites) while favoring the dominance of the Polytrichaceae family – which better tolerates open environmental conditions. It is also noteworthy that this area was the one with the lowest species richness (Wienskoski & Santos, 2022). Additional studies will be needed in that locality to evaluate the influence of environmental gradients and the availability of microhabitats on moss assemblages.

The areas located along roads, 2007 and “control road”, presented functional compositions more associated with open environments with high insolation (species with leaves having acute to acuminate apices, that may be hyaline, and with the apical region of the lamina distinctly pigmented or silvery – Glime, 2017b, c) and low moisture levels. Indeed, these areas were well represented by species of the family Bryaceae, whose principal identifying traits include a hyaline and piliferous leaf apex and special pigmentation. It must be pointed out that moss assemblages in the "control road" area are more similar to the 2007 area than to the "control trail". Proximity to the road can result in anthropic disturbances that impact bryophyte composition (Peñaloza-Bojacá *et al.*, 2018), such as the passage of motor vehicles, a high flux of pedestrian traffic, higher levels of solar radiation, and stronger winds (Aximoff & Rodrigues, 2011) – so that the presence of a road will expose the area to stress levels similar to those seen in post-fire sites such as area 2007.

According to Wienskoski & Santos (2022), the areas 2017 and "control trail" present greater proximity with moist sites in INP. Indeed, the assemblage of the 2017 area show the lowest predominance of character states related to stress. The most representative characteristics of the mosses present there were elongated leaf cells (indicative of greater agility for internal water transport - Glime, 2017c), and the presence of comal tufts. That same area also demonstrated the greatest representativeness of species of the families Bryaceae and Bartramiaceae, which produce large and inflated lamina cells (*e.g.*, *Philonotis hastata*). In the "control trail" area, the presence of certain traits linked to high-stress environments, such as regions of the lamina with special coloration (*e.g.*, dark colors tending to black) and leaves with wider costae, all suggest that, in *campos de altitude*, even areas with a low level of disturbance by fire present relevant environmental filters for acrocarpic mosses.).

The burning of the predominantly grassy vegetation in *campos de altitude* increases exposure to wind and solar radiation, which act as strong selective filters of temperature, luminosity, and humidity for mosses that could occupy the recently denuded areas, selecting species more functionally adapted for those conditions in the initial successional stages.

This study analyzed the different morphoanatomical characteristics that can enable acrocarpous mosses to overcome stressful environmental conditions and thrive in *campos de altitude*. Additional studies designed to evaluate the functionality of those traits under controlled conditions will be necessary to better elucidate the mechanisms of tolerance found in this large and pioneer plant group and the resilience of *campos de altitude* in the face of the climate changes currently underway.

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Authors' Contributions

Tibério da Silva Vale: Data curation; Formal Analysis; Investigation; Software, Visualization; Writing (original draft), Writing (review & editing). Wanessa Vieira Silva Menezes Batista: Investigation; Formal Analysis, Methodology; Software, Validation; Visualization, Writing – original draft; Visualization, Writing – review & editing. Luiz Ricardo dos Santos Tozin: Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing – original draft; Writing – review & editing. Nivea Dias dos Santos: Conceptualization; Data curation; Formal Analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Validation; Visualization; Writing – original draft; Writing – review & editing

Conflict of Interest

The authors declare no conflicts of interest.

Supplementary Material:

Table S1. Correlation coefficients between trait values and the CatPCA axes, explanatory variance of each of the axes, and eigenvalues. Stronger correlations with each axis are in bold.

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