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Original article

Post-fire effects on bryophytes in High-Altitude Fields

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ABSTRACT

High-Altitude Fields are ecosystems with high bryophyte abundances and diversities. One of the principal threats to these ecosystems are wildfires, which mainly affect terricolous species. Chronosequence studies can aid in understanding post-fire effects on bryophytes. We studied terricolous assemblages of bryophytes in the High-Altitude Fields of Itatiaia National Park (INP) by establishing three 20x1 m transects in five areas: three areas of a post-fire chronosequence (treatments 2017, 2007, and 2001) and two control areas. We analyzed the species richness, floristic composition, life-forms, and floristic similarities of those transects, identifying 27 species of mosses (18 genera; 11 families) and 26 species of liverworts (20 genera; 16 families). Ditrichaceae was the principal moss family and Cephaloziellaceae the principal liverwort family. The life-forms encountered were turf (43 %), weft (38 %), thalloid (10 %), and mat (9 %). Turf predominated among mosses (85 %), and weft among liverworts (62 %). Species richness and floristic compositions varied among the post-fire gradients. The grouping dendrogram and ordination diagram evidenced greater similarity among transects within the same area. However, there was no evident gradient of floristic composition along the post-fire gradient, and further studies will be needed to quantify environmental gradients and their influences on bryophyte composition.

Keywords: bryophytes, liverworts, mosses, High-Altitude Fields, *campos de altitude*, Brazilian páramos, Itatiaia National Park**,** anthropic disturbances, fire, chronosequence

Introduction

Understanding variations in species composition along environmental gradients has been one of the principal subjects addressed by ecologists (Blackburn & Gaston 2006; Hawkins & Diniz-Filho 2006), and many of those studies have examined the effects of natural or anthropic disturbances on species diversity and ecosystem functioning (Chapin *et al*. 2002; Isbell *et al.* 2011). Studies of ecological succession provide a means of understanding the roles of disturbances on the dynamics of plant communities and the processes associated with biodiversity losses, as well as detail the effects of environmental alterations and/or invasive species on natural ecosystems and thus aid restoration programs (Connell & Slatyer 1977; Prach & Walker 2011).

Studies of ecological succession examine temporal changes in biodiversity after disturbance impacts that

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modify abiotic factors, community structures, and ecosystem functioning (Morin 2011). Indirect observational approaches are most frequently utilized in those studies to understand the temporal dynamics of ecosystems, communities, and populations. That approach examines chronological sequences (chronosequences) in study areas to compare them along evolutive scales, thus allowing for long-term observations of ecological processes when there are records of the year/epoch of the initial disturbance and its subsequent history (Pickett 1989; Fukami & Wardle 2005; Walker *et al.* 2010).

High-Altitude Fields (*campos de altitude* or Brazilian Páramos) are well defined and fragile insular ecosystems located along the ridges of the principal mountain chains in southern and southeastern Brazil (Safford 1999). They occupy approximately 350 km^2 of territory in that country, and occur above the elevational limits of forest cover (between 1600 – 1800 and 2900 masl; Segadas-Vianna & Dau 1965). They are associated with the Atlantic Forest domain, and their vegetations are composed of open grassy fields with herbaceous and shrubby vascular plants, and high abundances of bryophytes (Safford 1999; Scarano 2002). The Itatiaia National Park (INP) in Rio de Janeiro State covers an area *ca*. 28, 084 ha (ICMbio 2021). It is the conservation area with the largest extension of High-Altitude Fields in Brazil, with *ca*. 10, 000 ha above 2000 masl (Safford 1999; Aximoff 2011), which represents approximately 36 % of the total area of the INP.

The INP holds a high diversity of bryophyte species with many threatened taxa and is considered one of the most important areas for bryophyte conservation in Brazil (Gradstein & Costa 2003; Costa *et al.* 2005; Costa & Santos 2009; Rezende 2015; Gonçalves & Santos 2018). The High-Altitude Fields in the park also contain many specialist species of liverworts and mosses specific to certain substrates, with a predominance of rupicolous and terricolous taxa (Gonçalves & Santos 2018). Although those areas are of high conservation interest, Gonçalves & Santos (2018) noted that many threatened species do not have records of recent collections, indicating the lack of studies about those species, and consequently, the risk of biodiversity and genetic bank losses due the lack of action plans for conservation.

It is estimated that 70 % of all fires recorded in recent decades in High-Altitude Fields in Rio de Janeiro State occurred in the INP, with extensive fires recurring with a triennial pattern (Aximoff & Rodrigues 2011; Aximoff 2011). That high incidence of wildfires is generally associated with anthropic actions mainly linked to agro-pastoral activities, constituting one of the principal pressures on those ecosystems (Aximoff *et al.* 2016). The INP is surrounded by municipalities linked to those traditional land-use practices, and the high levels of wildfires in its High-Altitude Fields are related to the extensive farm and pasture lands within and around the park (Richter 2004; Aximoff & Rodrigues 2011; Aximoff 2011).

Among the factors that facilitate the occurrence of wildfires in High-Altitude Fields is their dry and cold climate, especially during the austral winter, with strong winds and the presence of accumulated biomass (Safford 1999; Aximoff 2011). Wildfires provoke a cascade of secondary ecological succession events, and while the diaspores of many plants, animals and microorganisms can survive in the soil, the passage of those fire disturbances represents a severe threat to local biodiversity, with serious risks to endemic, threatened, and rare species (Walker *et al.* 2010; Peroni & Hernández 2011). Nonetheless, studies examining the effects of those disturbances on the vegetation dynamics within the park have been relatively rare (Safford 2001; Aximoff *et al.* 2016).

Although the floristic compositions of bryophytes in High-Altitude Fields are fairly well known (Gradstein & Costa 2003; Santos *et al.* 2014; Costa *et al.* 2015), there have been no studies on the effects of environmental gradients on those assemblages. We therefore sought to analyze species richness, floristic composition, life-forms, and evaluate how fire disturbance modulates the compositions of terricolous bryophytes assemblages along a post-fire chronosequence in the High-Altitude Fields of the INP.

Materials and Methods

Study area

The present work was carried out in High-Altitude Fields (areas above 2000 masl) in the Itatiaia National Park, which is located on the border between the Brazilian states of Rio de Janeiro and Minas Gerais (22°25’ S x 44°40’ W). The region has a tropical altitudinal climate, with a mean annual temperature of 11.5° C and mean rainfall rates near 1000 mm in the dry season and 2500 mm during the rainy season (December to February) (Segadas-Vianna & Dau 1965). The herbaceous shrub vegetation there is exposed to low temperatures, ice conditions, strong winds, and intense solar radiation, and grows on thin rocky soils that are generally very poor in nutrients (Safford 1999).

Sampling and studying the botanic material

The bryophytes were collected in five High-Altitude Fields areas: three in a post-fire chronosequence (treatments 2017, 2007 and 2001) and two control areas (trail = T and road = R). Three 20x1m transects were randomly established in each area, totaling 15 transects, and data, including collection period, latitude, and longitude were recorded (Tab. 1). The plants were collected on soil, a predominant substrate in High-Altitude Fields, as well as on rocky substrates. Considering the substrate specificity of many bryophytes, and as a way to standardize the sampling, we choose to work

Table 1. Data concerning the study areas in High-Altitude Fields in the Itatiaia National Park, RJ, Brazil. T = Trail; R = Road.

Treatment	Transect	Type	Collection	Latitude	Longitude	Altitude
2017	1	trail	jan/2019	22° 21' 58.6" S	44° 41' 40.5" W	2463 m
	2	trail	jan/2019	22° 21' 58.6" S	44° 41' 45.5" W	2473 m
	3	trail	jan/2019	22° 22' 0.7" S	44° 41' 50.3" W	2503 m
2007	1	road	mar/2018	22° 23' 02.4" S	44° 40' 57.1" W	2396 m
	2	road	jan/2019	22° 22' 57.4" S	44° 41' 06.9" W	2404 m
	3	road	mar/2018	22° 22' 53.4" S	44° 41' 12.7" W	2417 m
2001	1	trail	apr/2018	22° 23' 29.1" S	44° 40' 15.5" W	2355 m
	2	trail	may/2018	22° 23' 43.9" S	44° 40' 11.5" W	2393 m
	3	trail	jan/2019	22° 23' 35.2" S	44° 40' 12.1" W	2359 m
Control T	1	trail	jan/2019	22° 22' 59.4" S	44° 41' 59.0" W	2569 m
	2	trail	jan/2019	22° 22' 53.7" S	44° 42' 05.6" W	2561 m
	3	trail	jan/2019	22° 22' 48.4" S	44° 42' 09.7" W	2537 m
Control R	1	road	jan/2019	22° 22' 37.3" S	44° 41' 42.1" W	2419 m
	2	road	jan/2019	22° 22' 35.0" S	44° 41' 47.5" W	2431 m
	3	road	jan/2019	22° 22' 31.2" S	44° 41' 56.5" W	2432 m

only with terricolous bryophytes, which are most affected by fire disturbances. The specimens collected will be deposited in the bryophyte collection of the RBR herbarium at the Departamento de Botânica of the Universidade Federal Rural do Rio de Janeiro, Brazil.

Species identifications followed the specialized literature, principally Gradstein & Costa (2003) for liverworts and Costa *et al.* (2010) for mosses. The life-form classification was based on Mägdefrau (1982) and Bates (1998), not considering sub-classifications, but adding the thalloid life-form, which was previously considered a subgroup of mat.

Data analysis

We compared species richness along the post-fire gradient by analyzing the medians and quartiles of the transect data. The data was plotted as boxplot graphs using BioEstat 5.0 software (Ayres *et al.* 2007). Species frequencies were quantified in terms of their presence or absence in the transects. As such, a given species could be quantified up to three times per area (as each area had three transects) and from 1 to 15 times in the total study (five areas with three transects each, totaling 15 transects). That measure was chosen to avoid underestimating species that are difficult to see with the naked eye (and were only collected in the field due to their association with other, larger plants). We elaborated a matrix with the sampled areas and the frequencies of the different species as descriptors. That matrix was submitted to floristic dissimilarity analysis, using the Bray Curtis index. A second floristic matrix was elaborated in which the areas were considered samples and the frequencies of the species were considered descriptors. The floristic similarities among the transects were calculated using the Jaccard index with the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). Correspondence analysis was used to examine the variations in composition of the bryophyte species in the transects along the disturbance gradient. All of the multivariate analyses were run on Fitopac software (Shepherd 2010).

Multi-Response Permutation Procedures (MRPP) (Mielke & Berry 2007) were used to verify if the species compositions of the bryophytes among the different treatments were different. That test was performed using PCOrd 4.1 software (McCune & Mefford 1999). MRPP is a robust, nonparametric method that uses a similarity index (here, we used the Jaccard index) to test the null hypothesis that two or more predefined groups have equal compositions. The A index of MRPP describes the homogeneity within groups, varying between 0 and 1, where the most similar groups are those with the A index closest to 1 (McCune & Grace 2002).

Results

Species richness and floristic composition

A total of 666 specimens were analyzed (491 mosses and 175 liverworts). Fifty-three species of bryophytes were identified (38 genera and 27 families), including 27 mosses (18 genera and 11 families) and 26 liverworts (20 genera and 16 families) (Tab. 2). Those results excluded one abundant taxon in High-Altitude Fields, the genus *Campylopus*, which could not be securely identified due to its high plasticity and low morphological differentiation, preventing its separation into morphotypes. To reduce the error probability due wrong identification, we choose not to include this genus in the data analysis.

The area with the greatest species richness was the treatment of the 2007 burn (totalizing 31 spp.; 9 spp. exclusive), followed by control T (30; 4), control R (27; 3), treatment 2017 (21; 3), and treatment 2001 (12; 1). We found similar results considering median richness (Fig. 1). Ditrichaceae was the principal moss family, and it appeared in all of the 15 transects, followed by Bryaceae (14), Polytrichaceae (13), and Mniaceae and Pottiaceae (11 each); the principal liverwort family was Cephaloziellaceae (9), followed by Lepidoziaceae (8). There were variations in

Table 2. List of species, families, abbreviation, voucher and life-forms of mosses and liverworts identified in the study areas in the High-Altitude Fields of Itatiaia National Park, RJ, Brazil. Abbrev. = Abbreviation; T = Trail; R = Road; W. = Wienskoski *et al.* (collectors names).

Group	Family and species	Abbrev.	Voucher	LF	2017	2007	2001	T	R	Total
Mosses	Bartramiaceae			3	2	0	1	2	8	
Mosses	*Breutelia grandis* (Hampe) Paris	Bre gra	W. 6	turf	3	2	0	0	2	7
Mosses	*Philonotis hastata* (Duby) Wijk & Margad.	Phi has	W. 40	turf	1	0	0	1	0	2
Mosses	Bryaceae			2	3	3	3	3	14	
Mosses	*Anomobryum julaceum* (Schrad. ex P.Gaertn. *et al.*) Schimp.	Ano jul	W. 54	turf	0	2	3	2	3	10
Mosses	*Bryum arachnoideum* Müll. Hal.	Bry ara	W. 59	turf	0	3	0	0	2	5
Mosses	*Bryum argenteum* Hedw.	Bry arg	W. 38	turf	1	3	0	3	2	9
Mosses	*Bryum billardieri* Schwaegr.	Bry bil	W. 58	turf	1	3	0	2	1	7
Mosses	*Bryum capillare* Hedw.	Bry cap	W. 30	turf	2	2	0	1	0	5
Mosses	*Bryum subapiculatum* Hampe	Bry sub	W. 41	turf	1	0	0	0	0	1
Mosses	Ditrichaceae			3	3	3	3	3	15	
Mosses	*Ceratodon purpureus subsp. stenocarpus* Bruch & Schimp.	Cer pur	W. 64	turf	0	1	0	0	0	1
Mosses	*Chrysoblastella chilensis* (Mont.) Reimers	Chr chi	W. 55	turf	0	2	0	0	2	4
Mosses	*Cladastomum ulei* Müll. Hal.	Cla ule	W. 1	turf	3	3	3	3	3	15
Mosses	Fissidentaceae			0	1	0	0	0	1	
Mosses	*Fissidens anguste-limbatus* Mitt.	Fis ang	W. 75	turf	0	1	0	0	0	1
Mosses	Hedwigiaceae			0	2	0	1	1	4	
Mosses	*Hedwigidium integrifolium* (P. Beauv.) Dixon	Hed int	W. 60	weft	0	2	0	1	1	4
Mosses	Hypnaceae			0	2	0	0	0	2	
Mosses	*Isopterygium tenerifolium* Mitt.	Iso ten	W. 77	weft	0	2	0	0	0	2
Mosses	Mniaceae			2	3	2	2	2	11	
Mosses	*Plagiomnium rhynchophorum* (Hook.) T.J. Kop.	Pla rhy	W. 79	turf	0	1	2	0	0	3
Mosses	*Pohlia camptotrachela* (Renauld & Cardot) Broth.	Poh cam	W. 81	turf	1	2	0	2	2	7
Mosses	*Pohlia elongata* Hedw.	Poh elo	W. 174	turf	0	0	0	1	1	2
Mosses	*Pohlia papillosa* (Müll. Hal. ex A. Jaeger) Broth.	Poh pap	W. 7	turf	2	3	0	2	2	9
Mosses	Polytrichaceae			1	3	3	3	3	13	
Mosses	*Itatiella ulei* (Broth. ex Müll. Hal.) G.L. Sm.	Ita ule	W. 123	turf	0	0	2	3	1	6
Mosses	*Polytrichum angustifolium* Mitt.	Pol ang	W. 8	turf	1	0	0	2	1	4
Mosses	*Polytrichum commune* L. ex Hedw.	Pol com	W. 11	turf	1	2	1	1	2	7
Mosses	*Polytrichum juniperinum* Willd. ex Hedw.	Pol jun	W. 53	turf	0	3	1	1	2	7
Mosses	Pottiaceae			3	3	0	3	2	11	
Mosses	*Barbula indica* (Hook.) Spreng.	Bar ind	W. 57	turf	0	3	0	0	0	3
Mosses	*Leptodontium araucarieti* (Müll. Hal.) Paris	Lep ara	W. 62	turf	0	3	0	2	2	7
Mosses	*Leptodontium stellatifolium* (Hampe) Broth.	Lep ste	W. 4	turf	3	1	0	3	1	8
Mosses	Sphagnaceae			2	0	1	0	0	3	
Mosses	*Sphagnum brasiliense* Warnst.	Sph bra	W. 3	turf	2	0	1	0	0	3
Mosses	Thuidiaceae			0	2	0	0	1	3	
Mosses	*Thuidium pseudoprotensum* (Müll. Hal.) Mitt.	Thu pse	W. 65	weft	0	2	0	0	1	3
Liverworts	Anastrophyllaceae			0	0	0	0	1	1	
Liverworts	*Anastrophyllum tubulosum* (Nees) Grolle	Ana tub	W. 164	mat	0	0	0	0	1	1
Liverworts	Aneuraceae			2	0	0	1	0	3	
Liverworts	*Riccardia digitiloba* (Spruce ex Steph.) Pagán	Ric dig	W. 2	thalloid	1	0	0	0	0	1
Liverworts	*Riccardia fucoidea* (Sw.) Schiffn.	Ric fuc	W. 49	thalloid	1	0	0	1	0	2
Liverworts	*Riccardia glaziovii* (Spruce) Meenks	Ric gla	W. 246	thalloid	0	0	0	1	0	1
Liverworts	Arnelliaceae			0	0	2	2	1	5	
Liverworts	*Gongylanthus liebmannianus* (Lindenb. & Gottsche) Steph.	Gon lie	W. 127	mat	0	0	2	2	1	5
Liverworts	Balantiopsidaceae			0	0	1	0	0	1	
Liverworts	*Isotachis multiceps* (Lindenb. & Gottsche) Gottsche	Iso mul	W. 125	weft	0	0	1	0	0	1
Liverworts	Calypogeiaceae			1	0	0	1	0	2	
Liverworts	*Calypogeia laxa* Gottsche & Lindenb.	Cal lax	W. 264	weft	0	0	0	1	0	1
Liverworts	*Calypogeia peruviana* Nees & Mont.	Cal per	W. 48	weft	1	0	0	1	0	2
Liverworts	Cephaloziaceae			2	0	0	1	0	3	
Liverworts	*Cephalozia crossii* Spruce	Cep cro	W. 32	weft	2	0	0	1	0	3
Liverworts	Cephaloziellaceae			2	0	2	3	2	9	
Liverworts	*Cephaloziella divaricata* (Sm.) Schiffn.	Cep div	W. 161	weft	0	0	0	1	0	1
Liverworts	*Cephaloziella granatensis* (J.B. Jack) Fulford	Cep gra	W. 20	weft	2	0	2	3	1	8

Table 2. Cont.

Group	Family and species	Abbrev.	Voucher	LF	2017	2007	2001	T	R	Total
Liverworts	Fossombroniaceae			0	1	0	0	1	2	
Liverworts	*Fossombronia porphyrorhiza* (Nees) Prosk.	Fos por	W. 70	mat	0	1	0	0	1	2
Liverworts	Frullaniaceae			0	1	0	1	1	3	
Liverworts	*Frullania brasiliensis* Raddi	Fru bra	W. 203	weft	0	1	0	1	1	3
Liverworts	*Frullania dusenii Steph.*	Fru dus	W. 214	weft	0	0	0	0	1	1
Liverworts	Gymnomitriaceae			0	1	0	2	2	5	
Liverworts	*Marsupella microphylla* R.M. Schust.	Mar mic	W. 95	weft	0	1	0	2	2	5
Liverworts	Jungermanniaceae			0	1	0	2	1	4	
Liverworts	*Jungermannia amoena* Lindenb. & Gottsche	Jun amo	W. 280	mat	0	0	0	2	0	2
Liverworts	*Jungermannia hyalina* Lyell	Jun hya	W. 117	mat	0	1	0	2	1	4
Liverworts	Lejeuneaceae			0	2	0	0	0	2	
Liverworts	*Drepanolejeunea bidens* (Steph.) A. Evans	Dre bid	W. 115	weft	0	1	0	0	0	1
Liverworts	*Harpalejeunea schiffneri* S.W. Arnell	Har sch	W. 113	weft	0	1	0	0	0	1
Liverworts	*Lejeunea laetevirens* Nees & Mont.	Lej lae	W. 84	weft	0	1	0	0	0	1
Liverworts	*Microlejeunea bullata* (Taylor) Steph.	Mic bul	W. 115	weft	0	2	0	0	0	2
Liverworts	Lepidoziaceae			3	1	3	1	0	8	
Liverworts	*Kurzia capillaris* (Sw.) Grolle	Kur cap	W. 5	weft	3	0	3	1	0	7
Liverworts	*Telaranea diacantha* (Mont.) Engel & Merr.	Tel dia	W. 12	weft	3	1	2	1	0	7
Liverworts	Metzgeriaceae			0	1	0	0	0	1	
Liverworts	*Metzgeria scyphigera* A. Evans	Met scy	W. 69	thalloid	0	1	0	0	0	1
Liverworts	Pallaviciniaceae			1	0	0	0	0	1	
Liverworts	*Symphyogyna podophylla* (Thunb.) Mont. & Nees	Sym pod	W. 10	thalloid	1	0	0	0	0	1
Liverworts	Plagiochilaceae			0	0	0	0	1	1	
Liverworts	*Plagiochila exigua* (Taylor) Taylor	Pla exi	W. 202	weft	0	0	0	0	1	1

species compositions among the treatments. In the areas that had most recently experienced burning, the families that appeared in all three transects were Bartramiaceae, Ditrichaceae, and Pottiaceae among the mosses and Lepidoziaceae among the liverworts. The families that most appeared in the control transects among the mosses were Bryaceae (present in the three transects of control T as well as in the three transects of control R), Ditrichaceae (three and three), and Polytrichaceae (three and three). The family that most appeared in the control transects among the liverworts was Cephaloziellaceae (three and two) (Tab. 2).

Cladastomum ulei (Ditrichaceae) was the most abundant moss species, appearing in all 15 transects, followed by *Anomobryum julaceum* (Bryaceae; ten), *Bryum argenteum* (Bryaceae; nine), and *Pohlia papillosa* (Mniaceae; nine). Among the liverworts, the most abundant species were *Cephaloziella granatensis* (Cephaloziellaceae; appearing in eight transects), *Kurzia capillaris* (Lepidoziaceae; seven), and *Telaranea diacantha* (Lepidoziaceae; seven). In the area that burned most recently (2017), the moss species that appeared in all three transects were *Breutelia grandis* (Bartramiaceae), *Cladastomum ulei* (Ditrichaceae), and *Leptodontium stellatifolium* (Pottiaceae); the liverwort species that appeared in all three of those transects were *Kurzia capillaris* and *Telaraneae diacantha* (both Lepidoziaceae). The moss species that appeared in all three transects in the control areas (T/R) were *Anomobryum julaceum* (Bryaceae; two/three), *Bryum argenteum* (Bryaceae; three/two) and *Cladastomum ulei* (Ditrichaceae; three/three); the liverwort species that appeared in all three of the control transects was *Cephaloziella granatensis* (Cephaloziellaceae; three/one) (Tab. 2).

Life-forms

The life-forms encountered were turf (43 %), weft (38 %), thalloid (10 %), and mat (9 %) (Fig. 2). Turf predominated among the mosses (85 %) and weft among the liverworts (62 %) (Fig. 2), and both were present in all of the transects (Tab. 3). Turf was the principal life-form encountered in all of the treatments. There were few differences in life-forms between the control and disturbed areas. The mat life-form was not present in treatment 2017 (transects with humid substrates near lakes), thalloid was not encountered in treatment 2001 or in control R (the driest transects); all of the mosses in treatment 2001 were turf (the driest transects with the greatest edge effects).

Table 3. Frequencies of the life-forms and number of species of each life-form in the treatments of the High-Altitude Fields in the Itatiaia National Park, RJ, Brazil.

Life-forms	Frequency of the life-form						Numbers of species					
	2017	2007	2001	T	R	Total	2017	2007	2001	T	R	Total
Turf	3	3	3	3	3	15	13	18	7	15	16	24
Weft	3	3	3	3	2	14	5	10	4	10	9	19
Mat	0	1	2	2	1	6	0	2	2	3	3	4
Thalloid	1	1	0	1	0	3	3	1	0	2	0	5

Floristic similarities of the bryophyte assemblages

Few species were shared among all of the treatments, as can be seen in the dendrogram (cophenetic correlation

= 0.83). The floristically most distinct areas, according to the Bray Curtis index (dissimilarity), were treatments 2001 *x* 2007 (dissimilarity = 0.84), 2017 *x* 2007 (0.72), and 2001 *x* control R (0.72). The areas that shared the most species were control R and treatment 2007 (0.39). Those areas exclusively shared the species *Bryum arachnoideum*, *Chrysoblastella chilensis*, *Thuidium pseudoprotensum* (mosses), and *Fossombronia porphyrorhiza* (liverwort). It was possible to discern a pattern among the treatments in the ordination analysis (axes 1 and 2 = 65 % of the variation), where similarity was greater among areas with similar environmental gradients. There was a distinct separation of the trail areas (treatment 2017, treatment 2001, and control T) on the left side of the diagram, and the road areas (treatment 2007 and control R) on the right side. The areas that had not experienced fire disturbances (controls T and R)

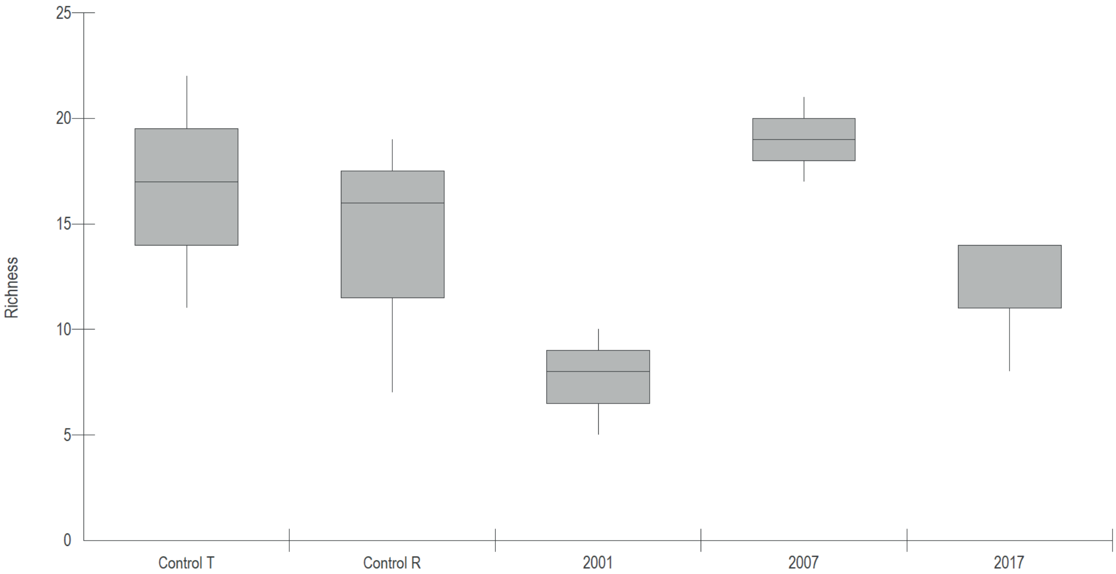

Figure 1. Box-plot of the median richness of three transects studied in the treatments (wildfires in 2017, 2007 and 2001) and controls (T and R) in the High-Altitude Fields of the Itatiaia National Park, RJ, Brazil.

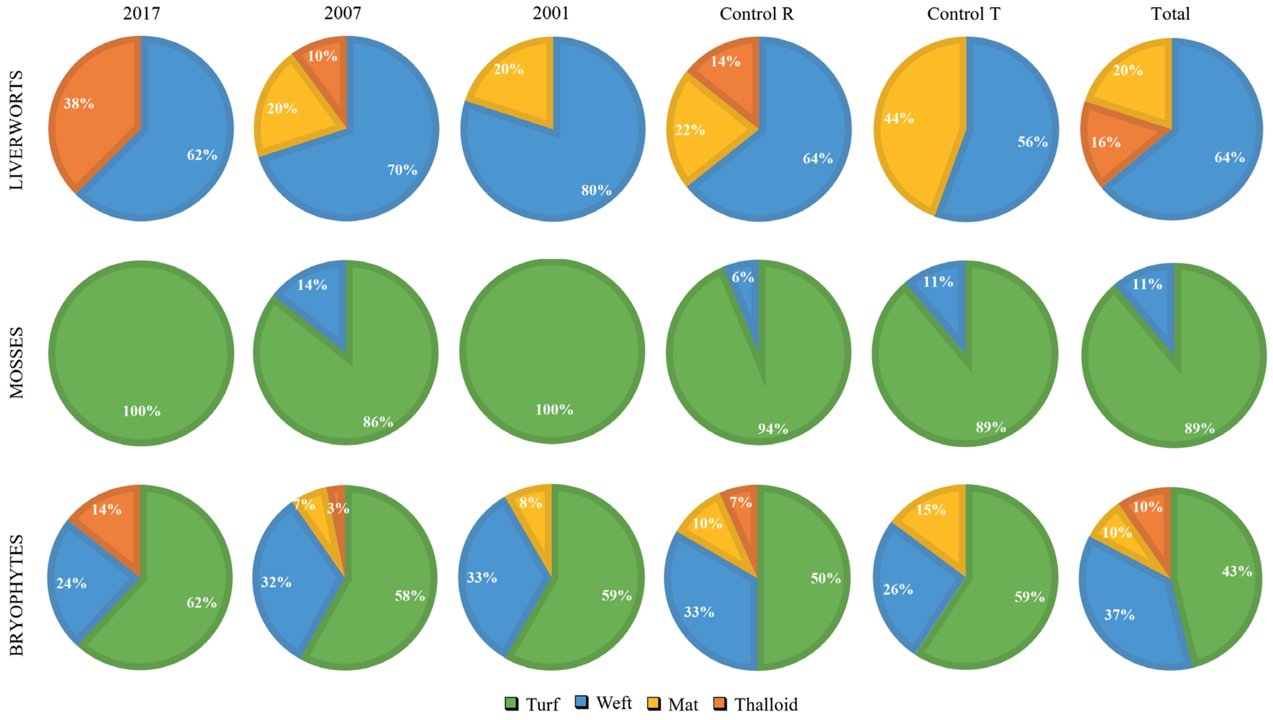

Figure 2. Proportions of the life-forms of bryophytes species (liverworts and mosses) identified for the areas studied in the High-Altitude Fields of the Itatiaia National Park, RJ, Brazil.

were closest in the ordination diagram. In relation to the transects close to the trails, there was a greater proximity among humid areas (treatment 2017 and control T) and a dryer site (treatment 2001).

The floristic similarities among the transects were low when the five areas (treatments 2017, 2007 and 2001, and control T and R) were compared. There was greater similarity among transects within the same area. The greatest similarity indices (> 0.5) were observed between transects 2001_1 *x* 2001_3 (Jaccard = 0.78), control T_2 *x* control T_3 (0.61), and control R_1 *x* control T_3 (0.55). The grouping dendrogram (cophenetic correlation = 0.87) evidenced the formation of three groups. The first group comprised two subgroups, one formed by the transects in the area that burned in 2007 and a control area (R_2), and another comprising the two transects in the control area near the trails (T_2 and T_3) and the control R_1. The second group also comprised two subgroups, one formed by the areas burned in 2017, which grouped with control area T_1, and another formed by two transects that burned in 2001 (transects 1 and 3). The third group was formed by an area that burned in 2001 (transect 2) and a control area (R_3).

The biplot diagram of the species ordination (axes 1 and 2 = 32 % of the variance), corroborated the pattern encountered in the dendrograms (transects generally grouped by their post-fire times). It is possible to determine which species predominated in the different treatments in that diagram (Fig. 3), such as *Barbula indica,* which only occurred in the 2007 transects, *Gongylanthus liebmannianus* and *Itatiella ulei* which only occurred in the more recent fire treatments (2017 and 2007), *Anastrophyllum tubulosum* which only occurred in control area R_1, and the thalloid liverworts, which only occurred in treatment 2017 (*Riccardia digitiloba*, *Riccardia fucoidea* and *Symphyogyna podophylla*) and in control area T (*Riccardia fucoidea* and *Riccardia glaziovii*), both of which are near water resources and have humid soils. Although the ordination analyses did not demonstrate cohesive groups and isolated all of the transects belonging to the same treatments, the MRPP demonstrated that floristic differences were greater between treatments than within treatments (A = 0.43; p = 0.001).

Discussion

The terricolous species sampled in this study represented 10 % of all bryophytes species in the INP (519 bryophyte species (213 genera and 81 families)) and 6 % of all bryophyte species known to Rio de Janeiro State (Costa *et al.* 2015) (Tab. 4). One possible explanation for that relatively low species richness percentage in the INP resides in the differing sizes of the areas (High-Altitude Fields represents only 36 % of the total area of the INP), their differing environmental heterogeneity, available microenvironments, and the substrates sampled. There is greater substrate variety available in the montane and alto-montane forests of the INP for colonization by bryophytes. Trees create environmental gradients (of luminosity, humidity, and temperature) and provide a high diversity of microenvironments and bryophyte species (Pócs 1982). The vegetation in the High-Altitude Fields of the INP is predominantly composed of grass species (Safford 1999),

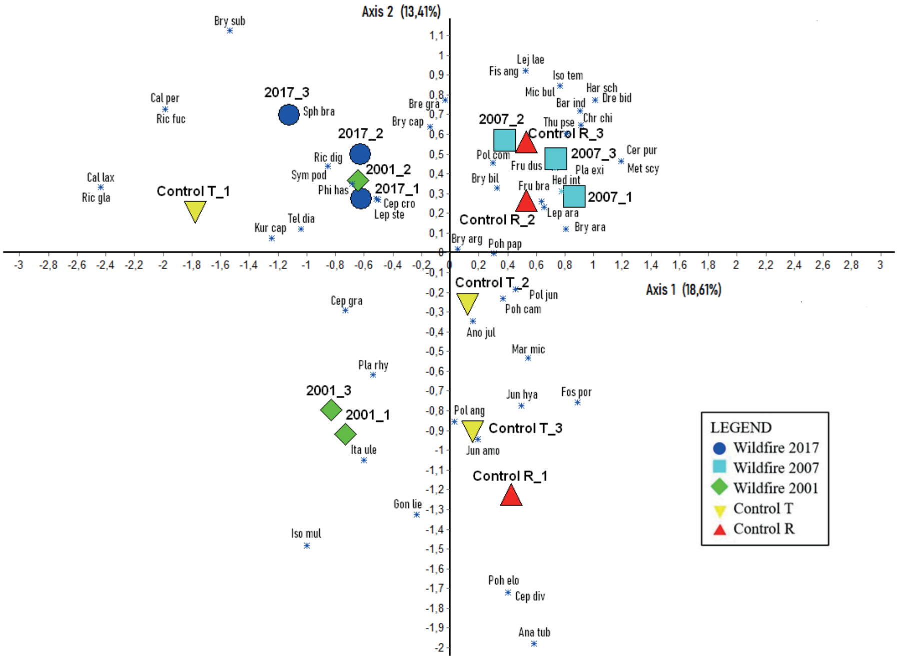

Figure 3. Biplot of the Correspondence Analysis of the floristic matrix of transects sampled, among treatments (wildfires in 2017, 2007 and 2001) and controls (T and R), in the High-Altitude Fields of the Itatiaia National Park, RJ, Brazil.

Table 4. Comparative table of the species richness of bryophytes in different locations throughout the world. The numbers in parentheses represent the relative proportions of species identified in the present study. Adapted from Costa *et al.* (2015).

Area	Mosses	Liverworts	References
Transects of this study	27	26	This study
INP High-Altitude Fields	179 (15 %)	128 (20 %)	Costa *et al.* (2015)
Itatiaia	289 (9 %)	230 (11 %)	Costa *et al.* (2015)
Rio de Janeiro State	519 (5 %)	370 (7 %)	Costa (2014), Costa & Peralta (2015)
Atlantic Forest	756 (3,6 %)	464 (5,6 %)	Costa (2009)
Brazil	878 (3 %)	638 (4 %)	Costa (2014), Costa & Peralta (2015)
Tropical America	2,600 (1 %)	1,350 (2 %)	Gradstein *et al.* (2001)
World	13,000 (0,2 %)	5,000 (0.5 %)	Gradstein *et al.* (2001)

making bryophyte establishment difficult (as those grasses intercept solar radiation and compete for space). As such, bryophytes predominantly occur on soils along the edges of open areas (trails and roads) and on rock outcrops (although those rocky environments were not sampled in the present study). Another factor that can explain the low bryophyte species richness in the High-Altitude Fields of the INP was our decision to sample only terricolous species (the group most affected by wildfires) and excluding rupicolous species (a large bryophyte group in that ecosystem). We verified that some disturbances, such as trails and road openings, have positive effects on High-Altitude Fields terricolous bryophyte diversity. The transects in areas with the greatest species richness (treatment 2007) were installed along roadsides, which are areas subject to greater edge effects and consequently have more open substrates that could support bryophytes. It is worth mentioning that although this disturbance makes possible the existence of microenvironments for bryophytes colonization, predatory tourism can represent a serious threat to the bryoflora.

As postulated by Connell (1978), intermediary disturbance levels can maintain a high diversity of species in sessile organisms communities. This premise was corroborated while we evaluated the post-fire effect over bryophytes, where the area affected by a fire in 2007 presented similar species richness as the control areas. The control areas, with higher species diversity, demonstrated differences in their richness and in their numbers of exclusive species. Although control area R was located near a road, its transects were on dryer substrates than those of control T (which had quite humid soils, similar to treatment 2017). That situation also helps explain why the area that was most recently burned (2017) had a higher species richness than other areas that had burned years before. High atmospheric humidity levels, presence of streams and lakes, in addition to a good conservation state of vegetation can possibly be factors which minimized negative impacts from existent disturbances in this region.

The principal families of mosses and liverworts that occur in the study area exhibit strategies that help them tolerate desiccation and/or escape stress conditions (whether water stress or burning). Life-forms such as turf (Bartramiaceae, Ditrichaceae, and Pottiaceae) and weft (Bartramiaceae and Lepidoziaceae) are examples of tolerance strategies: that allow the accumulation of water among the gametophytes; with the presence of papilla, which are cellular projections that aid in reflecting back sunlight and facilitating CO2 diffusion into the plants (Bartramiaceae, Ditrichaceae, and Pottiaceae); with leaves that twist when dry to protect the photosynthetic apparatus from strong incident light by exposing the thicker ventral surface (Ditrichaceae and Pottiaceae) (Vanderpoorten & Goffinet 2009; Glime 2017). In terms of attributes related to avoidance, some taxa have very small gametophytes (< 3 cm) (Ditrichaceae and Lepidoziaceae) and reduced leaves (Lepidoziaceae) (Glime 2017).

Breutelia grandis, *Cladastomum ulei*, and *Leptodontium stellatifolium* are species endemic to Brazil that occur only in mountainous regions (above 1000 masl) in the Atlantic Forest, while *Anomobryum julaceum*, *Bryum argenteum,* and *Pohlia papillosa* are widely distributed globally (Flora do Brasil 2020 2020). All of those mosses have gametophytes with morphologically adapted leaves: (i) *Breutelia grandis*, *Cladastomum ulei*, and *Leptodontium stellatifolium* have papilla that aid in reflecting light and facilitating the diffusion of CO2 (although *Cladastomum ulei* does not always show papilla); (ii) *Leptodontium stellatifolium* and *Pohlia papillosa* produce gametophytes with leaves that twist when dry, thus protecting the photosynthetic layer from high incident light levels; (iii) *Anomobryum julaceum* and *Bryum argenteum* have imbricate leaves that protect their dorsal surfaces from strong sunlight, the latter species also has hyaline apices that reflect light and aid in capturing water and CO2; (iv) *Cladastomum ulei* has twisted and imbricate leaves when dry; and, (v) *Breutelia grandis* has densely tomentose caulidia that aid in capturing humidity (Costa *et al.* unpubl. res; Vanderpoorten & Goffinet 2009; Glime 2017; Flora do Brasil 2020 2020). Additionally, *Cladastomum ulei* displays a highly plastic phenotype, with gametophytes being seen with leaves robust or thin, imbricate or twisted when dry, with or without papilla, and greenish yellow to dark green leaves varying from subulate to lanceolate, costae percurrent to short excurrent, and with a mucron. Those morphological variations probably aid the plants in adjusting to environmental filters acting in the High-Altitude Fields of the INP and would explain their occurrence in all of the transects. Those characteristics, together with the turf life-form that predominates among the most abundant species, provides them with protection against desiccation (Bates 1998) – a fundamental strategy for surviving and reproducing in High-Altitude Fields where the light intensity is very strong (Segadas-Vianna & Dau 1965; Safford 1999).

The liverworts *Cephaloziella granatensis*, *Kurzia capillaris*, and *Telaranea diacantha* are widely distributed in Brazil, as well is in the neotropical region (the latter two species also occur in paleotropical regions) (Gradstein & Costa 2003; Flora do Brasil 2020 2020). Those liverworts likewise have adaptations to protect them from desiccation, as their gametophytes are small and their life-forms weft, which allows them to grow hidden within the leaf litter and among other plants, where solar light levels and temperatures are more amenable. Additionally, the leaves of *Kurzia capillaris* and *Telaranea diacantha* are divided into filiform segments (Gradstein & Costa 2003) that increase their surface to volume ratios and thus aid in obtaining water by osmosis. That strategy of increasing surface to volume ratios is also observed with *Cephaloziella granatensis*, which has papilla and bifid leaves.

The predominance of the turf life-form among mosses reflects the fact that it is a typical life-form of acrocarpous terricolous mosses. In extreme climates that life-form aids in: (i) hydric control, as liquid water can be held in the spaces between the gametophytes, and (ii) temperature regulation, as the plants are able to retain more water and diminish their internal temperatures as compared to the external environment (Glime 2017). Turf colonies also diminish their surface to volume ratios, which aids in avoiding desiccation (as only the apical leaves are exposed to the external environment). When dry, those leaves generally twist or assume imbricate positions, thus further diminishing their surface areas and protecting the photosynthetic apparatus against full desiccation (Bates 1998; Vanderpoorten & Goffinet 2009).

High numbers of weft species are associated with the type of substrate, since on less rigid substrates, gametophytes cannot strongly adhere to them (Bates 1998). In this study, weft life-forms were associated with escape strategies. Their high frequency in High-Altitude Fields in the INP (principally among liverwort taxa) is probably related to their facility for occupying shady microhabitats, as in mixed in other bryophytes – reflecting the difficulty of encountering shaded habitats in that ecosystem. In that way, the species can protect themselves from intense solar radiation in less-exposed environments and remain hydrated for longer periods of time.

While we encountered differences in species richness and floristic composition, there was no evident gradient of floristic composition along the post-fire gradient, so that other environmental filters must be acting to drive bryophyte distribution. The presence of vegetation borders provide larger areas for the establishment of bryophytes in the High-Altitude Fields, with fewer vascular plants to compete with them for space and light, although that greater exposure to sunlight demands efficient strategies to avoid desiccation. Additionally, the presence of humid environments alters the composition, richness, and life-forms of bryophytes in High-Altitude Fields, thus generating distinct plant assemblages and ecological strategies.

Although previous studies of fire effects in High-Altitude Fields have been undertaken (Safford 2001; Aximoff 2011; Aximoff & Rodrigues 2011; Aximoff *et al*. 2016), they did not address the effects of environmental gradients on bryophyte assemblages. Here we verified that disturbances caused by wildfires affect bryophytes assemblages, causing changes in species diversity and represents risks to endemic, threatened, and rare bryophyte species which occur in the area. Additional studies will therefore be needed to focus on quantifying the environmental gradients in High-Altitude Fields (*e.g.*, trail widths, distances from water resources, soil compaction, etc.) and their influences on bryophyte species composition.

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