Artigo

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A comparative study of temporal variation of two epiphytic bryophytes in a central Amazonian white-sand forest, Brazil

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ABSTRACT - (A comparative study of temporal variation of two epiphytic bryophytes in a central Amazonian white-sand forest, Brazil). We evaluated the local population dynamic of two epiphytic species, *Syrrhopodon helicophyllus* and *Thysananthus amazonicus*, over six years from 2014-2020, both before and after the fire event which occurred in the white-sand forest (*Campinarana*) located in Central Amazon. We did not observed an overall differences on colony abundance on the host tree over time before the fire event in 2019. However, colony abundances shifts along the vertical gradient towards mesic microenvironment which allow to persist during the El Niño event of 2015-2016, and recovered in the following years. Moreover, we observed that colonies of both bryophyte species drastically declined after the fire event in 2019, leading to a complete loss of the species in some of the host tree studied. The direct impacts of climate change with an increased fire and drought events in Central Amazon forests will result in the loss of epiphyte local biodiversity, especially in the unique isolated white-sand forests.
Keywords: Brazil, climate change, forest fire, population dynamics, white-sand forest

RESUMO - (Um estudo comparativo da variação temporal de duas briófitas epífitas em uma floresta de campinarana da Amazônia central, Brasil) Avaliamos a dinâmica populacional local de duas espécies epífitas, *Syrrhopodon helicophyllus* e *Thysananthus amazonicus*, ao longo de seis anos de 2014-2020, tanto antes quanto depois do incêndio que ocorreu na Campinarana localizada na Amazônia Central. Não observamos diferenças gerais na abundância de colônias na árvore hospedeira ao longo do tempo antes do evento de incêndio em 2019. No entanto, a abundância de colônias muda ao longo do gradiente vertical em direção ao microambiente mésico, o que permite persistir durante o evento El Niño de 2015-2016, e recuperado nos anos seguintes. Além disso, observamos que as colônias de ambas as espécies de briófitas diminuíram drasticamente após o incêndio em 2019, levando à perda completa das espécies em algumas das árvores hospedeiras estudadas. Os impactos diretos das mudanças climáticas com o aumento de incêndios e secas nas florestas da Amazônia Central resultarão na perda da biodiversidade local epífita, especialmente nas florestas isoladas como as Campinaranas.
Palavras-chave: Brasil, dinâmica populacional, floresta de areia branca, incêndio florestal, mudanças climáticas

Introduction

White-sand forests (*Campinaranas*) are habitats characterized by acid poor nutrient sandy soils, with short stature vegetation stature and high luminosity (Cordeiro *et al*. 2016). Plant communities are highly diverse in this habitat (Vicentini 2004, Ferreira 2009, Boelter *et al*. 2014, Adeney *et al.* 2016, Guevara *et al*. 2016), with composition changes over the Amazon landscape (increasing beta diversity with geographical distance) (Costa *et al*. 2019). Paleoclimatic studies suggest these open habitats, such as Campina and Campinaranas, expanded in the Amazon forest due to drier climatic conditions during the Last-Glacial maximum, which lead to the specialized biota observed today (Zular *et al*. 2019). However, land use and climate changes are causing an increase in local forest fire events (Fonseca *et al.* 2017), threatening Amazon biodiversity to an eventual loss of unique habitats and species, such as the ones in white-sand forests.

Increasing annual climate oscillations in the Amazon forest have been predicted using climatic models, where dry seasons will become prolonged each coming year (Gloor *et al*. 2015), and could become unpredictably drier during El Niño events (Jiménez-Muñoz *et al.* 2016). Furthermore, prolonged droughts will lead to an increase in the frequency of forest fires, and when not controlled, it could potentially devastate forest structure and its function across a vast region (Alencar *et al*. 2015, Brando *et al*. 2019). This

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scenario will definitely impact the survivability of terrestrial plant groups, such as epiphytic bryophytes, that depend on humid microclimates to survive (Sonneleitner *et al.* 2010).

Forest fires impact bryophyte populations by making drastic changes in forest structure or the complete depletion of local habitats. The degree of severity of a fire event is a crucial determinant of the post-fire persistence or fate of species and their substrates (Esposito *et al*. 1999; Pharo *et al.* 2013; Wills *et al*. 2018). Fire severity will determine the recovery trajectory of plants after such disturbances (Pharo *et al.* 2013; Wills *et al*. 2018), if local refugia, suitable habitats, are not completely destroyed allowing species to recolonize the disturbed area (Pharo & Lindenmayer 2009; Wills *et al.* 2018). Most of studies addressing the impact of forest fire have focus on recent fires on dry habitats in the mediteranean and in Australia (Esposito *et al*. 1999; Pharo *et al*. 2013; Wills *et al.* 2018), or in temperate forest with disturbances dating more than a century ago (Paquette *et al.* 2016). As deforestation and man induced forest fire increases in the Amazon forest during the last decades, it makes it imperative to understand the impacts of such recent disturbances on plant populations.

Bryophytes are highly sensitive to microclimate conditions changes and habitat quality, which make them good environmental indicators (Frego 2007; Silva & Porto 2014; Hernández-Hernández *et al*., 2019). Bryophytes species habiting a myriad of substrates, are lost as forest fragmentation intensifies (Alvarenga *et al*. 2009; Zartman 2003), and this impact persists over decades (Sierra *et al*. 2019). With current climate becoming hotter and drier in the Amazon forest, it is likely that local extinction increases during the dry season as well (Zartman *et al*. 2015). Also, observation data combine with species distribution modelings points to a local shift or eventual lost of epiphytic bryophytes with further decline of suitable habitats in the Atlantic forest (Farias *et al*. 2017; Alvarenga et al. 2010). However, species response to these disturbances should be taken with cautiousness and it should be pointed out that species might respond differently to fragmented habitat and climate change depending on their specific species traits (Sierra *et al*. 2019; Souza *et al.* 2019).

The bryophyte species *Syrrhopodon helicophyllus* Mitt. (Calymperaceae) and *Thysananthus amazonicus* (Spruce) Steph. (Lejeuneaceae), are an understory epiphyte specialist and canopy epiphyte specialist respectively (Mota de Oliveira 2018; Pereira 2019). Both species are common and locally abundant on the tree species *Aldina heterophylla* Spruce ex Benth (Leguminosae: Papillonoideae). The tree *A. heterophylla* is restricted to Amazonian white-sand forest (Ireland 2005, Cardoso *et al*. 2013, Mari et al. 2016; Queiroz *et al*. 2015), and harbors a high abundance of non-vascular and vascular epiphytes. The local abundance of this species allows us to study the epiphytic populations at a local scale, avoiding differences in environmental conditions between areas of Campinarana. Also, the abundances of epiphytes give the opportunity to evaluate the long-term dynamics of epiphytic bryophyte populations between host trees, and local shift within host tree strata (i.e., lower stem, inner canopy and outer canopy).

In the present article, we evaluated local population dynamics of two epiphytic species (*Syrrhopodon helicophyllus* and *Thysananthus amazonicus*) over six years of monitoring. Specifically we look for changes in colony density between host tree and between host tree strata over time, and related to changes in climatic conditions and a specific fire event occurred in the local area in the late 2019. We expect that the total epiphyte colony number did not vary between host trees over time, despite temporal variation in temperature and precipitation. However, major disturbance events such as local fire will drastically reduce host colony numbers or cause the local extinction of populations with the fate of the substrate. Secondly, between tree strata we expect temporal variation in the colony number, as epiphytes will shift along the vertical gradient in relation to changes in climatic conditions (temperature and precipitation), or with major disturbances.

Materials and Methods

Study site - We study populations of epiphytic bryophyte in a white-sand forest located between the municipalities of Manacapuru and Novo Airão, in the State of Amazonas, Brazil (3°02’53.1”S, 60°45’38.5”W). The study area covers a patch of white-sand forest on the AM-352 highway point Km-33, entering through the Ramal do Mineiro (figure 1). It is characterized by a low vegetation composed of shrubs and herbs ranging from 0.2 to 5 meters height. There are several isolated large trees of the species *Aldina heterophylla* (figure 1) in open areas or near the forest edge. All host trees studied were in rather open areas to avoid differences in microclimate conditions due to variable forest canopy (Alvarenga *et al*. 2010).

Field sampling - Five neighboring host trees (within an area of ~2 km in diameter) were marked and measured to characterize the sizes of each tree. Their size range varied between 18-87 cm DBH (diameter at breast height 1.30 m). Epiphytic bryophyte populations were monitored during the months of February 2014, 2016, 2018, and 2020. In November 2019, an anthropogenic fire occurred in the area, which caused the death of one of the five marked phorophytes, the other four phorophytes persisted thus permitting demographic census of the remaining four phorophytes to be conducted in February 2020, three months after disturbances.

Seasonal climate in the central Amazon is characterized by a long wet season from December to late July, and a short dry season from August to November. To evaluate the climatic conditions during the monitoring years, we obtain daily and monthly meteorological data from the Instituto Nacional de Meteorologia (IMNET) of Brazil, from the Manacapuru (3°17’41.0”S 60°37’42.0”W; 36 masl), and Manaus (3°06’13.0”S, 60°00’56.0”W; 48 masl) stations. The meteorological station of Manacapuru is the closest station to our study site, but it has missing data for some periods of interest. Due to this reason we use data from the meteorological station of Manaus. Comparing the data of both stations, they present similar records of temperature, precipitation and relative humidity for the years 2012 to 2020.

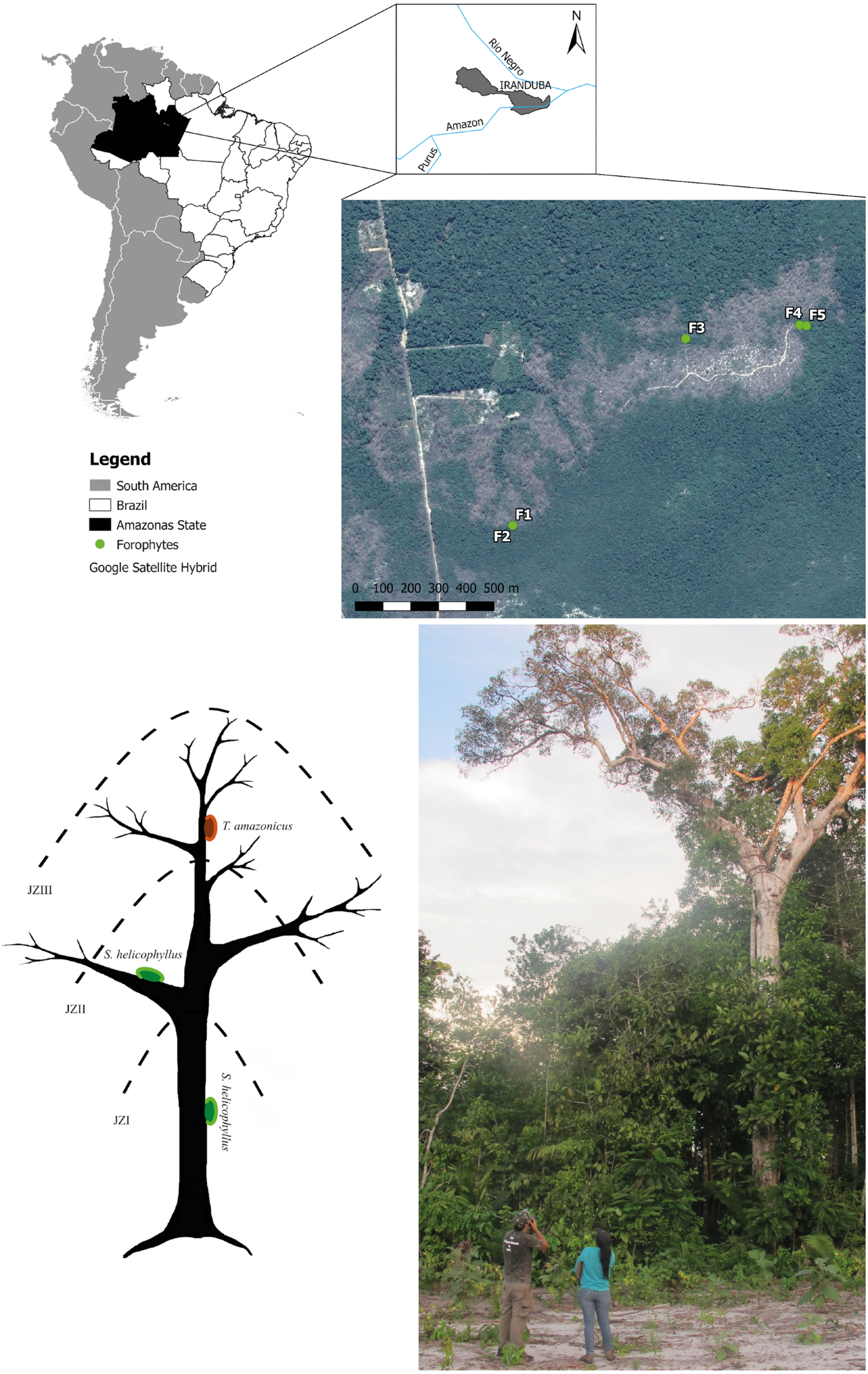

Figure 1. Study site in the Amazonas State in Brazil. Location of the area in the Central Amazon showing highway marker Km 33 on the AM-352 highway (Lat. 3°02’53.1”S, Long. 60°45’38.5”W), between the municipalities of Manacapuru and Novo Airão. Sampling demographic censuses of (*Syrrhopodon helicophyllus* Mitt. *and Thysananthus amazonicus* (Spruce) Steph.) on *Aldina heterophylla* Spruce ex Benth. JZI: stem, JZII: inner canopy and JZIII: outer canopy.

We used single rope climbing techniques (Rapel) following the procedures of Mitchell et al. (2002) to access the tree vertical zones in all study host trees. Tree vertical zones were separated based on the Johansson vertical zones (Johansson 1974), trunk (JZI), inner canopy (JZII), and/or the outer canopy (JZIII) (figure 1). When needed, we used binoculars to count colonies in branches in the outer canopy. Both species are easily distinguished by their habit, where *S. helicophyllus* form large compact green turf, while *T. amazonicus* form large brown upright or pendulous patches. The number of colonies in each tree stratum was counted by considering each isolated patch as a colony. The total number of colonies in each vertical strata and the complete number of colonies in each tree were quantified (Table supplementary 1).

Statistical analyses - The normality of the data was tested using the Shapiro-Wilcox test, which showed a normal distribution of the number of colonies (W=0.9569, p=0.1308). We tested for differences in the abundance of the colonies of the two species of bryophytes (*S. helicophyllus* and *T. amazonicus*), between years and across the vertical gradient using repeated-measures ANOVA with an unbalanced design. Differences in the mean number of colonies observed between sampling years and tree strata were addressed using Tukey's multiple means comparisons, with a 95% family-wise confidence level.

We used a Generalized Linear Model with a Poisson distribution to look for colony density (as a response variable) shifts along the host tree vertical gradient over time. Vertical zones and the sampled year were treated as predictive variables, and the density of epiphyte colonies of the species *S. helicophyllus* and *T. amazonicus* as response variable. Our model considered each stratum in the vertical profile nested in each phorophyte. The intercept and slope in the model were treated randomly, assuming that the rate of effect of the predictor variables may be different between the strata. All analyses were performed using the free software R (version 3.2.5) (2020) and the *car* package (Fox & Weisberg 2019).

Results

We observed a significant decrease in the number of epiphyte colonies from the year 2014 to 2020 (ANOVA: F_3 = 8.0516; *p-value* = <0.001) (figure 2 a; table 1). This was mainly due to the significant decrease in the year 2020 compared to the previous year, as a result of a forest fire in the year 2019, Tukey test: *p-value* = <0.001 (Table supplementary 2). Variation in the total number of colonies between 2014 and 2018, was not significantly different based on the Tukey test: *p-value* = 0.3-0.9 (figure 2 a; table supplementary 2).

We also observed different colony density distribution along the vertical gradient (ANOVA: F_2 = 16.4777; *p-value* = <0.001) (figure 2 b; table 2). Total colony density was greater in the inner canopy (JZII), than in the stem and outer canopy (Tukey test *p-value* = <0.001; Table supplementary 3). However, both species showed different vertical distribution patterns (ANOVA: F_2 = 5.0859; *p-value* = <0.01), where *S. helicophyllus* was slightly more abundant than *T. amazonicus* in the tree stem (Tukey test *p-value* = 0.86). On the other hand, *T. amazonicus* was more abundant in the outer canopy than *S. helicophyllus* (Tukey test *p-value* = 0.1). In the inner canopy (JZII) of the phorophyte, the two species were equally abundant, Tukey test: *p-value* = 0.92 (Table supplementary 4).

We look for shifts of epiphyte colony density along a vertical gradient and related it to climate variation and a fire event in 2019 using General Linear Mixed model (figure 2 c; table supplementary 5). The climate record for the region of the study area showed that during the El Niño event of 2015-2016, temperatures were higher, and monthly precipitation and relative humidity were lower relative to other years between 2012 and 2020 (figure 3). Results indicate the both species shift along the vertical gradient to mesic zones (Z = 3.698, *p-value* = <0.001) during hotter and drier years (figure 3). *Syrrhopodon helicophyllus*, shifted to the lower zone of the tree trunk during the hotter and driest years between 2015-2016, and to the inner canopy in 2018. Whereas, *T. amazonicus* colonies slightly decreased since 2014, shifting from the inner to the outer canopy during this period. In the year 2020, three months after the fire event in all the vertical zones were a decrease in colony density (Z = -3.237, *p-value* = <0.01). However, less impact was observed on the inner canopy of the phorophytes for the two species. In the inner canopy, colonies persist in the phorophyte, while in the stem and outer canopy, local extinction of most or all colonies was observed (figure 2 c).

Discussion

We carry out a comparative study of the population temporal variation of two epiphytic bryophyte species in an open white-sand forest (Campinarana) in the Amazon Basin. Our results showed that populations of both species *S. helicophyllus* and *T. amazonicus* were more abundant in the inner crown of *Aldina heterophylla* (56% of the colonies). The middle zones this is the inner tree crown present mesic microenvironment that favour the colonization of vascular and non-vascular epiphytes (Bataghin *et al*. 2012; Alvarenga *et al*. 2010), because of the balance between the level of luminosity and the water availability (Köster *et al*. 2009). Each of the species that we studied, have distinct preference towards either the tree trunk (JZI) in *S. helicophyllus*, while *T. amazonicus* in the outer tree crown (JZIII), where they were more abundant respectively. Differences in species physiological adaptations have been addressed at large scale with epiphyte communities (Alvarenga *et al*. 2010; Mota de Oliveira 2018). Mota de Oliveira (2018), analysed liverwort epiphytic community in light of species traits and concluded that traits such as lobule and dark pigmentation favor the persistence in the outer canopy, both characteristics are present in *Thysanthus amazonicus*. The species *S. helicophyllus*, as all the members of the family Calymperaceae, present leaves with costa and hyaline cells at the base. These traits are related to enhance the capacity to conduct and retain water in stressful conditions. White-sand forests are open habitats and making the lower tree trunk and inner canopy prone to stressful conditions as well.

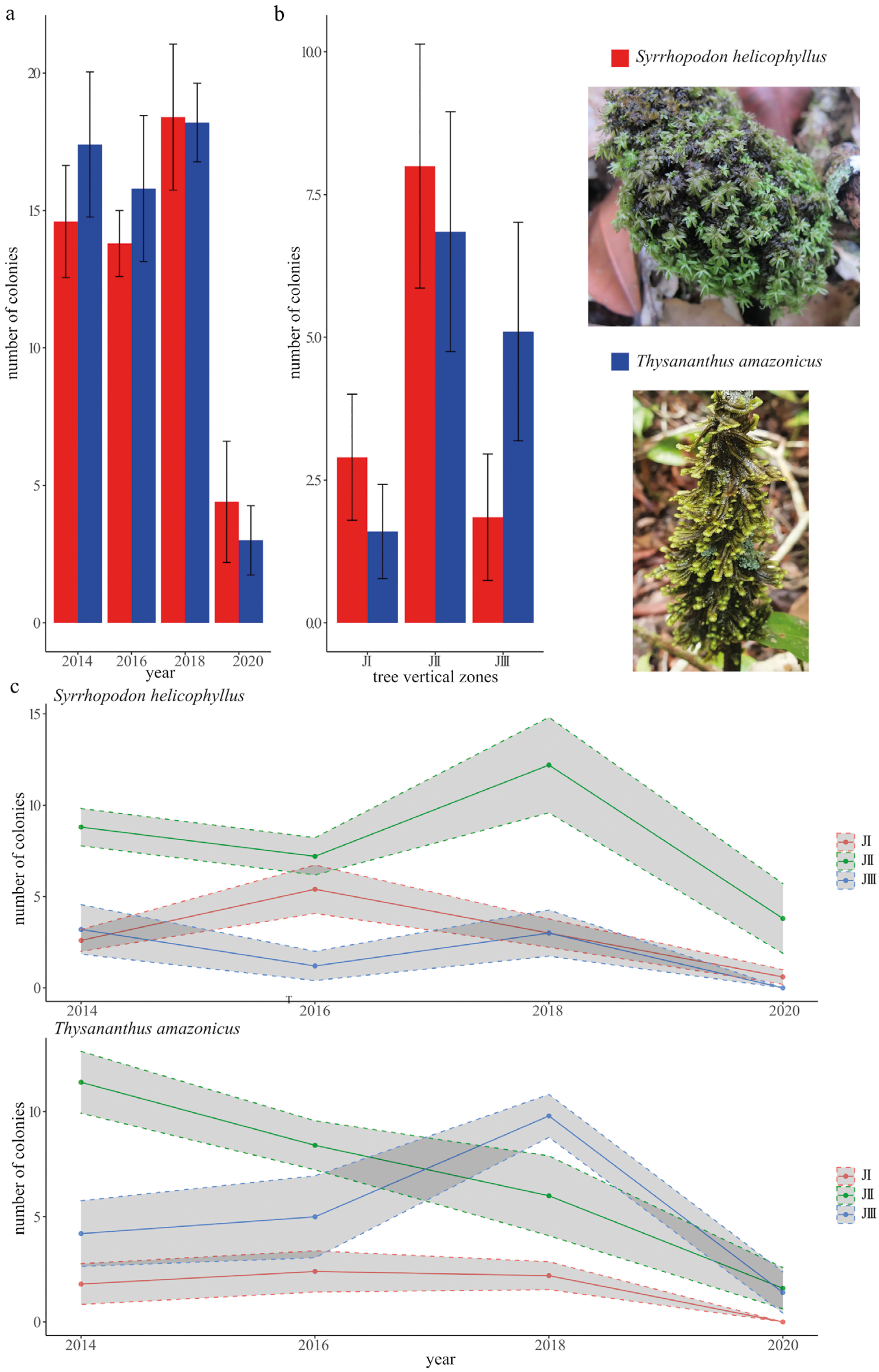

Figure 2. Differences in the number of colonies of the epiphytic species *Syrrhopodon helicophyllus* Mitt. and *Thysananthus amazonicus* (Spruce) Steph. a. The total number of colonies of *Syrrhopodon helicophyllus* Mitt. and *Thysananthus amazonicus*(Spruce) Steph.on the phorophyte *Aldina heterophylla* Spruce ex Benth. for the six years. b. Number of colonies of *Syrrhopodon helicophyllus* Mitt. and *Thysananthus amazonicus* (Spruce) Steph. on the three vertical strata of the phorophyte *Aldina heterophylla* Spruce ex Benth. c. Alterations in the number of colonies of *Syrrhopodon helicophyllus* Mitt. and *Thysananthus amazonicus* (Spruce) Steph. on the three vertical strata of the phorophyte *Aldina heterophylla* for the six years.

Table 1. Summary of the statistics showing two-way ANOVA difference in epiphyte colonies on different years sampled for the two species. Significant results are presented in bold.

	Sum sq	df	F	p
Intercept	1065.8	1	48.5006	**0.001**
Year	530.8	3	8.0516	**0.001**
Species	19.6	1	0.8919	0.3520
Year : Species	28.2	3	0.4278	0.7344
Residual	703.2	32		

Table 2. Summary of the statistics showing two-way ANOVA difference in epiphyte colonies on different tree vertical strata sampled for the two species. Significant results are presented in bold.

	Sum sq	df	F	p
Intercept	168.2	1	12.8045	**0.001**
Species	16.90	1	1.2865	0.259
Tree strata	432.90	2	16.4777	**0.001**
Species: tree strata	133.62	2	5.0856	**0.01**
Residual	1497.50	114		

We also look at the response of the epiphytic colonies in a short-term after a fire event in the study area. Local population extinction of epiphytes are determined by the substrate availability and suitable microclimate (Snäll *et al*. 2003; Zartman *et al*. 2012), conditions that lead to their evolution and niche specialisation (Laenen *et al*. 2014). If the severity of the fire is low, local populations will decline immediately, but epiphyte populations will recover on the remaining available substrate and local refugia (Pharo & Lindenmayer 2009; Esposito *et al.* 1999). The ability to shift to upper tree strata, as suitable habitats in the lower tree trunk or understory fate after the fire, allow population persistence on the host tree as observed here. However, the loss of the host tree immediately results in the local extinction of these epiphytic bryophytes.

Overall epiphyte colony variation and shift along a vertical gradient

First we look if host tree colony abundance varied between the year monitored and if this was related to changes in regional meteorological conditions. With the higher temperatures, lower precipitation and lower relative humidity during the El Niño event of 2015-2016, both species had a small reduction in colony density in 2016 when compared to 2014, with a latter increased in the year 2018.

Second, as overall colony abundance did not vary on the host tree over time, we explore if shifts along the vertical gradient allow population persistence in the presence of drastic climatic change, such as the increased temperature and drought in 2015-2016. Indeed, during harsher conditions associated with changes in regional meteorological conditions, the colony density of both species shift towards more mesic environments to avoid long term desiccation. With favorable conditions in the coming years both species showed an overall recovery, by increasing in tree zones that declined after the El Niño events.

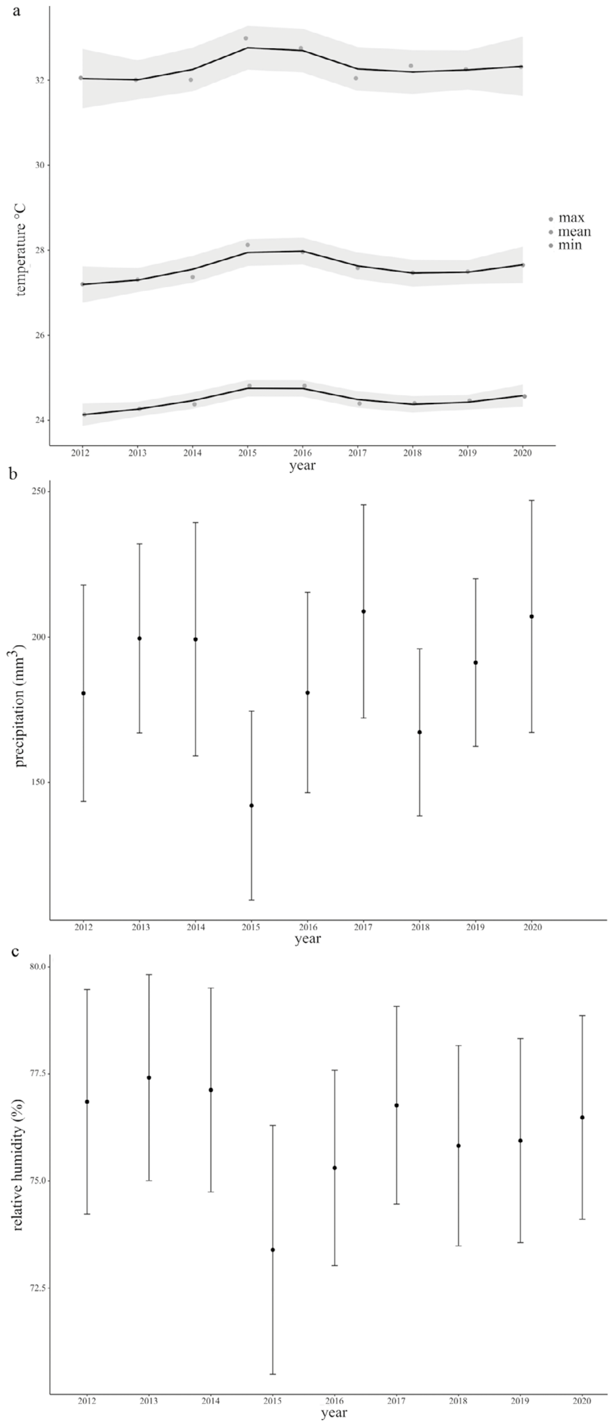

Figure 3. Meteorological record of each year from 2012-2020 for the region of study, including data from the meteorological station of Manacapuru and Manaus, Amazonas State, Brazil.

An study with the moss species *Campylopus lamellatus* during the El Niño of 2015-2016, also showed a negative response to the prolonged drought event in that year (Silva *et al.* 2020). In the following rainy season, they observed a positive investment in biomass and photosynthetic recovery in the same moss species. The recovery in colony density observed here and the physiological recovery observed by Silva *et al*. (2020), points that bryophytes might be able to recover after a drought event, as long as favorable environmental conditions proceed such drought events.

However, large disturbances associated with drought events, such a fire might cause the complete depletion of local habitats. To address this, we evaluated the epiphytic populations after an specific fire event in 2019. Short after, we observed a drastic decline in colony abundance in both species.This decline in colony abundance after a fire event is associated with impacts on the vegetation structure and host plant mortality. With the decline of populations and destruction of substrate after a fire, will impede the recolonization and recovery of epiphytes (Wills *et.al*. 2018). This point out that populations will be severely impacted as intense fire events associated with drier conditions continues to destroy mature forest. However, how epiphyte populations will recover and their long-term response needs further work using a wider geographical sampling.

Conclusions

The El Niño event of 2015-2016 caused severe drought in northern Brazil and vegetation mortality in the Amazon forest (Jiménez-Muñoz *et al*. 2016; Brito *et al.* 2017; Leithold *et al*. 2018; Silva Junior *et al*. 2019). Our present study lacks a large sampling to address the influence of this drastic climate variability on epiphytic bryophyte at a large scale. Nevertheless, our data indicate that epiphytes are affected by the changes in temperature and hydrological meteorological regimens and might be able to recover. However, it is preoccupying if epiphytic populations will be able to recover as record temperatures and drought become more frequent, in addition to the increase in fire events (Jiménez-Muñoz *et al.* 2016).

Campinarana are highly threatened by habitat destruction (such as deforestation, commonly associated with wood and sand extraction), and by uncontrolled forest fires causing the mortality of the fauna and flora of the region (Alencar *et al.* 2015, Brando *et al*. 2019). Climate changes driven by anthropogenic activities will result in larger and more frequent severe drought and fire events in tropical forest (Fonseca *et al.* 2017). As climate change advance without efficient conservation and mitigation plans, the loss of biodiversity will accelerate causing the loss of unique species and habitats in the Amazon forest.

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Conflict of interest

This article doesn't cause conflict of interest.

Authors Participation

Marta Regina Pereira: data collections, data analysis and writing

Adriel M. Sierra: data collections, data analysis and writing

Jair Max Furtunato Maia: data analysis and writing

Ana Sofia Sousa de Holanda: data collections, data analysis and writing

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Supplementary material

Table Supplementary 1. Raw data indicating the number of colonies of each species per phorophyte evaluated from 2014 - 2020, in a central Amazonian white-sand forest, Brazil.

	2014		2016		2018		2020	
Phorophyte ID	S. helicophyllus	T. amazonicus	S. helicophyllus	T. amazonicus	S. helicophyllus	T. amazonicus	S. helicophyllus	T. amazonicus
1	10	22	12	26	9	23	3	6
2	14	12	16	14	14	16	8	5
3	15	16	14	12	22	18	11	4
4	21	12	18	26	23	14	0	0
5	12	25	11	13	16	18	0	0

Table supplementary 2. Differences (*diff*) in the epiphytic number of colonies between years sampled, in a central Amazonian white-sand forest, Brazil. Tukey multiple comparisons of means 95% family-wise confidence level. Lower and upper ranges are presented in the table. Significant differences are highlighted in bold.

Year	*Diff*	Lower	Upper	*p-value*
2016-2014	-1.2	-6.652	4.252	0.933
2018-2014	2.3	-3.152	7.752	0.67
2020-2014	**-12.3**	**-17.752**	**-6.847**	**>0.001**
2018-2016	3.5	-1.952	8.952	0.324
2020-2016	**-11.1**	**-16.552**	**-5.647**	**>0.001**
2020-2018	**-14.6**	**-20.052**	**-9.147**	**>0.001**

Table supplementary 3. Differences (*diff*) in the epiphytic number of colonies between tree vertical strata sampled, in a central Amazonian white-sand forest, Brazil. Tukey multiple comparisons of means 95% family-wise confidence level. Lower and upper ranges are presented in the table. Significant differences are highlighted in bold.

Tree vertical strata	*diff*	Lower	Upper	*p-value*
JII-JI	**5.17**	**3.191**	**7.158**	**>0.001**
JIII-JI	1.225	-0.758	3.208	0.31
JIII-JII	**-3.95**	**-5.933**	**-1.96**	**>0.001**

Table supplementary 4. Differences (*diff*) in the epiphytic number of colonies for the species *Syrrhopodon helicophyllus* Mitt. and *Thysananthus amazonicus* (Spruce) Steph., between tree vertical strata sampled, in a central Amazonian white-sand forest, Brazil. Tukey multiple comparisons of means 95% family-wise confidence level. Lower and upper ranges are presented in the table. Significant differences are highlighted in bold.

Species: tree vertical strata	diff	Lower	Upper	*p-value*
T. amazonicus :JI-S. helicophyllus :JI	-1.3	-4.622	2.022	0.866
S. helicophyllus :JII-S. helicophyllus :JI	**5.1**	**1.777**	**8.422**	**>0.001**
T. amazonicus :JII-S. helicophyllus :JI	3.95	0.627	7.272	0.01
S. helicophyllus :JIII-S. helicophyllus :JI	-1.05	-4.372	2.272	0.941
T. amazonicus :JIII-S. helicophyllus :JI	2.2	-1.122	5.522	0.395
S. helicophyllus :JII-T. amazonicus :JI	**6.4**	**3.077**	**9.722**	**>0.001**
T. amazonicus :JII-T. amazonicus :JI	**5.25**	**1.927**	**8.572**	**>0.001**
S. helicophyllus :JIII-T. amazonicus :JI	0.25	-3.072	3.572	0.999
T. amazonicus :JIII-T. amazonicus :JI	3.5	0.177	6.822	0.032
T. amazonicus :JII-S. helicophyllus :JII	-1.15	-4.472	2.172	0.915
S. helicophyllus :JIII-S. helicophyllus :JII	**-6.15**	**-9.472**	**-2.827**	**>0.001**
T. amazonicus :JIII-S. helicophyllus :JII	-2.9	-6.222	0.422	0.124
S. helicophyllus :JIII-T. amazonicus :JII	**-5**	**-8.322**	**-1.677**	**>0.001**
T. amazonicus :JIII-T. amazonicus :JII	-1.75	-5.072	1.572	0.647
T. amazonicus :JIII-S. helicophyllus :JIII	3.25	-0.072	6.572	0.059

Table supplementary 5. General Linear Mixed model summary statistics showing differences in epiphyte colonies on different tree vertical strata sampled between years sampled, in a central Amazonian white-sand forest, Brazil. Significant results are presented in bold.

	Estimate	Std.Error	Z-value	*p-value*
(Intercept)	0.7885	0.2132	3.698	**0.001**
Year 2016	0.5725	0.2666	2.147	**0.1**
Year 2018	0.1671	0.2897	0.577	0.5
Year 2020	-1.9924	0.6155	-3.237	**0.01**
JII	1.5241	0.2353	6.478	**0.001**
JIII	0.5199	0.2692	1.931	**0.05**
Year 2016:JII	-0.8309	0.3063	-2.713	**0.01**
Year 2018:JII	-0.2713	0.3237	-0.838	0.4
Year 2020:JII	0.6731	0.6525	1.032	0.3
Year 2016:JIII	-0.7494	0.3611	-2.076	**0.1**
Year 2018:JIII	0.3809	0.3558	1.071	0.28
Year 2020:JIII	0.3274	0.7407	0.442	0.65

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