ACTA
AMAZONICA

http://dx.doi.org/10.1590/1809-4392202402883

BIODIVERSITY AND CONSERVATION | ORIGINAL ARTICLE

Exploring local phenological and phenotypic variation of mosses (Bryophyta) in two common Amazonian habitats

Anna Kelly Nogueira Campos da SILVA, Tales ALVES JÚNIOR, Charles E. ZARTMAN*

Instituto Nacional de Pesquisas da Amazônia, Programa de Pós-Graduação em Botânica, Av. André Araújo, 2936, CEP 69037-375 Manaus, AM, Brazil.

* Corresponding author: chaszartman@gmail.com

ABSTRACT

Species variation in relation to habitat differences may offer valuable insights into understanding population divergence and speciation itself. In central Amazonia, phenotypic and phenological variation of four bryophytes - *Octoblepharum albidum*, *Octoblepharum pulvinatum*, *Leucobryum martianum* and *Pilosium chlorophyllum* - were investigated among white-sands and *terra-firme* plateaus to examine whether habitat differences relate to trait variation. In three of the four species, sexual expression was significantly more restricted temporally in the drier habitat type (white-sands forest) than that observed in more mesic, terra-firme plateau forests. Contrary to global patterns of reproductive behavior for bryophytes, male expression was notably more prevalent than female expression for three of the four species. Furthermore, significant infra-specific phenotypic variation among habitat types associated with multiple measured traits (e.g., total leaf length, apex length, base width) illustrate the evolutionary potential of Amazonian bryophytes in the framework of habitat differentiation. Future priorities should focus on resource allocation dynamics and ecophysiology in a phylogenetic context to better understand the role of habitat differentiation in speciation processes among Amazonian bryophytes.

KEYWORDS: adaptation, bryophytes, habitat heterogeneity, morphometry, speciation

Explorando a variação em características fenológicas e fenotípicas locais de musgos (Bryophyta) entre dois habitats comuns da Amazônia

RESUMO

Variações em espécies, quando associadas às diferenças de habitat, podem oferecer insights valiosos para a compreensão de processos de divergência populacional. Variações fenotípicas e fenológicas de quatro briófitas, *Octoblepharum albidum*, *Octoblepharum pulvinatum, Leucobryum martianum* e *Pilosium chlorophyllum* foram investigadas entre ambientes de areias brancas e platôs de terra firme na Amazônia central, para examinar se a diferenciação de habitat está correlacionada com as características mensuradas. Em três das quatro espécies, a expressão sexual foi significativamente mais restrita temporalmente no tipo de habitat mais seco (floresta de areias brancas) do que a observada nas florestas de terra-firme. Ao contrário dos padrões gerais de expressão sexual para briófitas em todo o mundo, a expressão anteridial foi mais dominante para três das quatro espécies. Ademais, variações fenotípicas infraespecíficas significativas observadas entre os habitats, quando associadas com as múltiplas características mensuradas – por exemplo, comprimento total da folha, comprimento do ápice e largura da base – ilustra o potencial evolutivo das briófitas Amazônicas no contexto de diferenciação de habitat. As prioridades futuras devem se concentrar em estudos acerca da dinâmica de alocação de recursos e ecofisiologia destas plantas em um contexto filogenético, visando entender melhor o papel da diferenciação de habitat nos processos de especiação entre as briófitas amazônicas.

PALAVRAS-CHAVE: adaptação, briófitas, heterogeneidade de habitat, morfometria, especiação

INTRODUCTION

Variation in biotic and abiotic components, referred to as environmental heterogeneity, is a key evolutionary force in shaping phenotypic (e.g., the set of expressed characteristics), and phenological (e.g., temporal cycles of growth and reproduction) traits among plant populations (Baythavong and Stanton 2010). Heterogeneous environments are often epicenters for speciation processes, as the varying conditions act synergistically on population selection and adaptive processes (Fine 2015; Stiling 2002), thus catalyzing incipient speciation (Coyne and Orr 2004). Exploring phenological and phenotypic trends in populations subject to diverging environmental pressures may offer insights into life history processes and contribute with predictive information

CITE AS: Silva, A.K; Alves Júnior, T.; Zartman, C.E. 2025. Exploring local phenological and phenotypic variation of mosses (Bryophyta) in two common Amazonian habitats. *Acta Amazonica* 55: e55bc24288.

regarding adaptational changes at multiple spatial scales (Jägerbrand *et al.* 2005; Mallet *et al.* 2009; Pereira *et al.* 2013).

Bryophytes, small, non-vascular plants with ephemeral life history strategies, are second only to angiosperms in global terrestrial plant richness, keystone contributors of ecosystem services in most of the earth's major biomes, and models for autecological studies (Vanderpoorten and Goffinet 2009; Rousk & Villareal 2024). Their generally broad distributions and wide ecological amplitudes make them ideal for addressing effects of environmental pressures on selection processes (Pócs, 1982; Gradstein 1992; Gradstein *et al.* 2001; Bowker *et al.* 2000; Zartman *et al.* 2015). For example, pressures exerted by contrasting conditions demonstrably promote phenotypic and phenological variations among individuals (Stark 2002), including fertilization rates and sex ratios (Maciel-Silva and Válio 2011; Maciel-Silva et al. 2012; 2013; Glime2021).

The Amazon Rainforest is an important biodiversity hotspot, and a primary source of lineages for other neotropical regions (Antonelli *et al.* 2018). It is a heterogeneous biome, with an array of vegetation types, such as "*Terra-firme*" forests comprised of ombrophilous, non-flooded forests which vary in structure and floristic composition over large geographic scales (Pires and Prance 1985; ter Steege et al. 2006). Within this matrix of *terra-firme* forests are patches of drier, oligotrophic white-sands habitats denominated "*Campinas*" or "*Campinaranas*" occurring near blackwater streams, and seasonally flooded blackwater rivers (Capurucho *et al.* 2020).

Amazonian plant diversity is roughly estimated to be ca. 60,000 species (Lewinsohn and Prado 2005; ter Steege *et al.* 2016; Cardoso *et al.* 2017). For bryophytes, the Amazon harbors the second largest species richness of any Brazilian Biome, hosting more than one-third (574 species) of the Nation's bryoflora (Costa *et al.* 2020). Studies focusing on the influence of habitat heterogeneity on Amazonian bryophytes have typically been conducted at the level of quantitative floristics and community analyses (Mandl *et al.* 2009; Oliveira and ter Steege 2015; Sierra *et al.* 2018; Costa *et al.* 2020; Cerqueira *et al.* 2021), while comparative studies at the level of populations incorporating phenotypic and phenological data are, to our knowledge, nonexistent.

In this study, we aimed to conduct a meso-scale investigation of the morphometric and phenological patterns among populations of four ecological generalist bryophyte species in two common Amazonian habitats: white-sands (*Campinarana*), and plateau *Terra-firme* forests. Considering the markedly different environmental conditions attributable to these habitat types (Adeney *et al.* 2016), we set out to test the hypothesis that temporal patterns of gametangial expression and phenotypic attributes associated with vegetative characters differ among populations of these contrasting environments. Specifically, the greater solar radiation and lower humidity levels of white-sands forests would be reflected, for example, in temporally constricted intervals of bryophyte gametangial expression, in combination with reduced surface area of photosynthetically active structures such as gametophytic leaf surfaces. These predictions arise from previous studies showing seasonal effects on the expression and maturation of gametangia associated with variation in local humidity for tropical bryophytes across an elevation gradient (Maciel-Silva and Válio 2011). Furthermore, evidence from experimental studies on infra-specific phenotypic plasticity for vascular plants demonstrate inverse relations among leaf size and solar radiation (Pelabón *et al.* 2013) suggesting that bryophyte populations of lower statured, white-sands forests characterized by open canopies may be composed of smaller leaf phenotypes (e.g., reduced apices, reduced bases, and reduced total leaf length).

MATERIALS AND METHODS

Study Area

This study was conducted in the municipality of Presidente Figueiredo, Amazonas, Brazil (Figure 1), along the Sussuarana trail: a 4.5 km pathway adjacent to Balbina Village and the Balbina hydroelectric dam. The trail encompasses distinct phytophysiognomies such as terra-firme *plateaus* – clayey upland forests with relatively closed/denser canopies when compared to other formations in the area, such as white-sands vegetations including *Campinaranas* (Perigolo *et al.* 2017; Komura *et al.* 2021). These white-sands areas, like others alongside the Uatumã River, occupy ancient river terraces positioned between the river's modern floodplains and the terra-firme *plateaus*, which surrounds the small, differentiated, isolated patches of sandy vegetation (Demarchi *et al.* 2021).

The region experiences a tropical wet climate (Köppen-Geiger: Af), with an average annual temperature of 27 °C and average annual rainfall of 1,920 mm (Beck *et al.* 2018, Resende *et al.* 2019). The rainy season (November to March) is characterized by an average monthly rainfall of 230 mm, with greater rainfall intensity in March, during which time the temperature ranges from a minimum of 26°C to 30°C. The dry season (May to September) has an average monthly rainfall of 92 mm and temperatures ranging from 27°C to 33°C, with the driest month being September. April and October are months of transition between the wet and dry seasons (INMET, 2018).

Focal species and field sampling

Four bryophyte species, *Octoblepharum albidum* Hedwig, *Octoblepharum pulvinatum Mitt.* (Octoblepharaceae), *Leucobryum martianum* (Hornsch.) Hampe. (Dicranaceae) and *Pilosium chlorophyllum* (Hornschuch) Müller Hal. ex Brotherus (Stereophyllaceae), were chosen for study – Illustrations and photographs of the four species can be found in Figure 2 – as they are common Neotropical ecological generalists which share similar substrates (rotten logs and decaying organic matter).

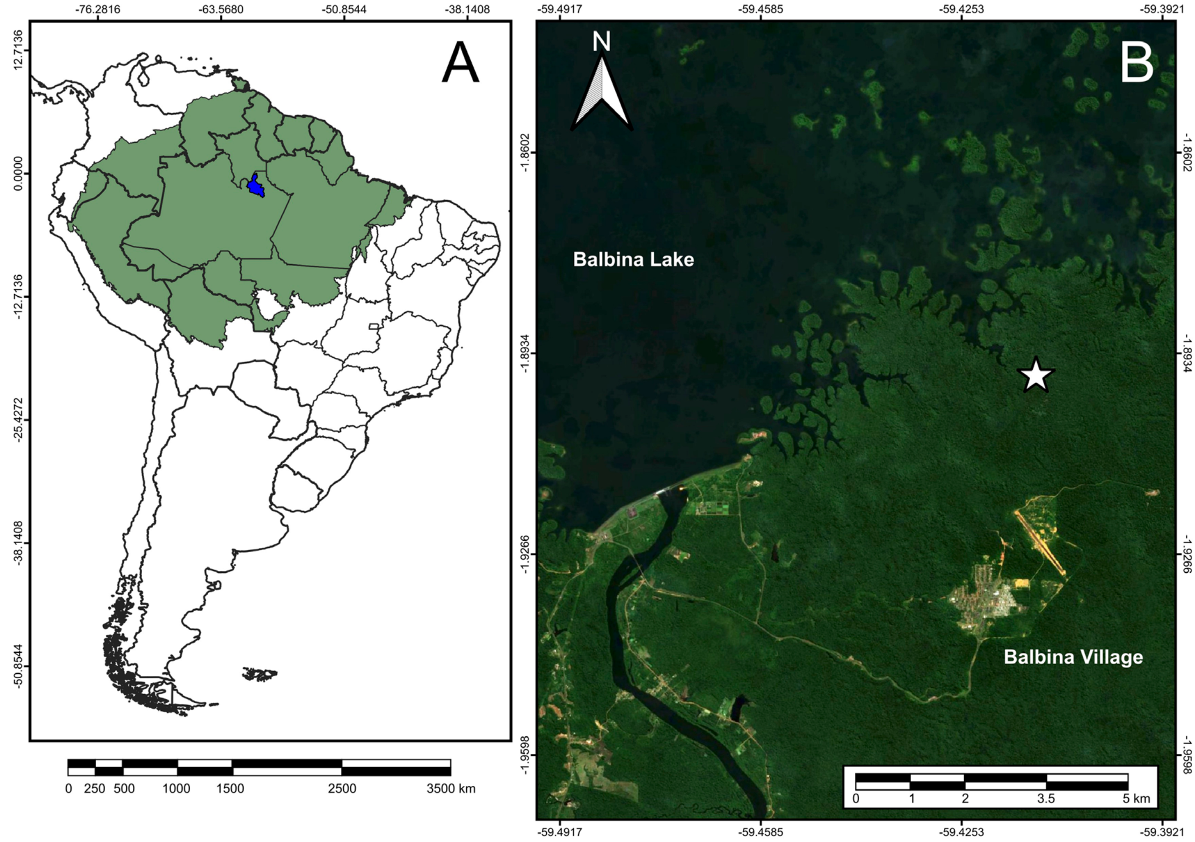

Figure 1. Map of the study area at the Sussuarana Trail, central Amazon. **A**: Approximate location of the study area within the Amazon biome (in Green), and city of Presidente Figueiredo (in Blue). **B**: Satellite imagery (Sentinel-2) of the Sussuarana Trail surroundings, with the trail location being marked with a white star. The tick marks represent SIRGAS 2000 / UTM Zone 21S projected coordinates.

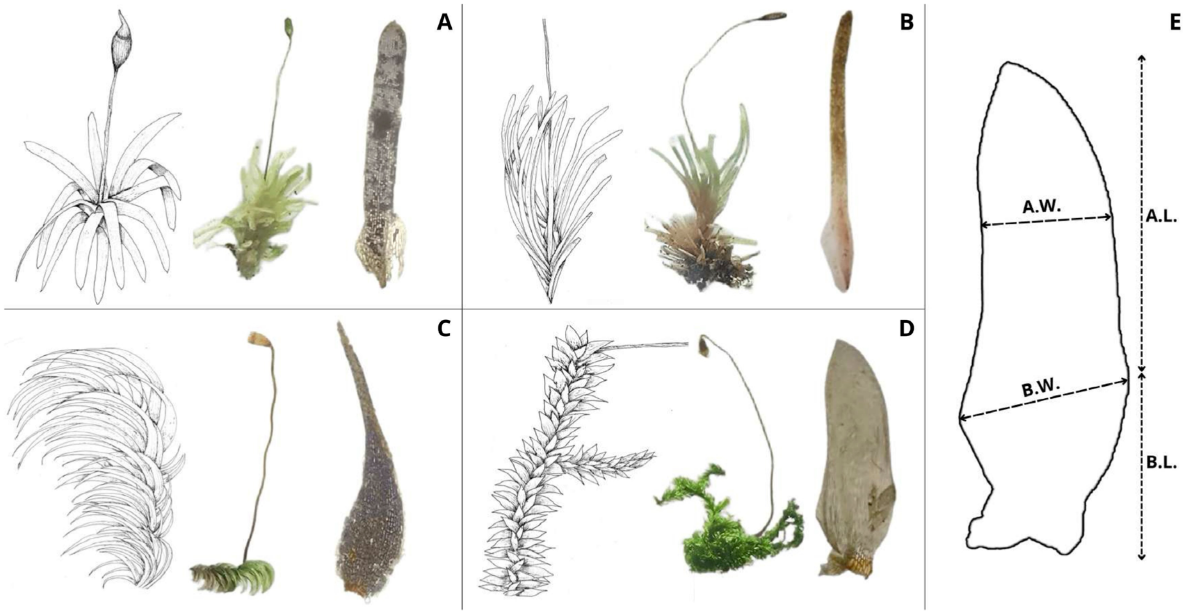

Figure 2. Illustrations and images of the focal species (habit and leaves). **A**: *Octoblepharum albidum* Hedwig; **B**: *Octoblepharum pulvinatum* Mitt; **C**: *Pilosium chlorophyllum* (Hornsch.) Müll. Hal.; **D**: *Leucobryum martianum* (Hornsch.) Hampe.; **E**: Example of morphometrical measurements (AW = apical width, BW = basal width, BL = basal length, AL = apical length, TL = the total length taken across the sum of AW and BW). Illustrations: Anna Kelly N. C. da Silva.

They are characterized as monoicous (autoicous), apart from the dioicous *L. martianum* (Costa and Peralta 2015; Oliveira-da-Silva and Ilkiu-Borges 2016; dos Santos *et al*. 2020).

A 5 cm² sample was collected for each of the four species from five populations once a month in both white-sands and upland forests (n = 40 monthly samples). The collections were made at the end of every month for one year (October to September 2016-17). Populations were initially marked with numbered stakes and were at least 15 m distance from each other. The specimens were deposited at the INPA Herbarium (INPA 0201185 to INPA 0201222).

Morphometry

From each sample, three gametophytes were randomly picked from which three leaves were separated for measurement with the use of a magnifying glass, tweezers and needles. Subsequently, leaves were rehydrated with tap water, and placed on slides for five measurements: AW = apical width (measured from one edge to the other in the apical region), BW = basal width (measured from one edge to the other in the basal region), BL = basal length (length from the shoulders, the widest part of the leaf, to the end of the blade), AL = apical length (measured from the tip of the leaf to the shoulders), TL = the total length obtained by adding AW and BW (Fischer *et al*. 2007; Luna and Velasco 2008) (Figure 2). Measurements were made with the use of a Leica DM2500 optical microscope (Leica Microsystems, Ernst-Leitz-Straße, Germany).

Phenology

From each sample, ten gametophytes were randomly chosen for phenological studies (Greene 1960; Stark 2002; Laaka-Lindberg 2005). If present, perichaetial and perigonial branches as well as the antheridia and archegonia harbored therein were counted and their phenophase classified based on the criteria detailed in Table 1.

Data analysis

Phenotypic variation among individuals from upland and white-sands forests was assessed by means of multivariate analysis, using principal component analysis (PCA) on standardized traits (centered and scaled to unit variance to account for differing measurement scales) – via a correlation matrix. In addition, an Analysis of Similarity (ANOSIM) was performed to test groupings (Supplementary Material, Appendix S1), where the R statistic varies from -1 to 1, and proximity to 1 reveals greater differences among groups (Clarke, 1993). To determine whether the morphometric variables of each species differ among upland and white-sands forests, a t-test was also performed. Additionally, the Mantel test was performed to assess whether geographic distance is correlated with phenotypic variation by comparing two dissimilarity matrices: a spatial distance matrix (Euclidean) and another representing floristic distances (Bray-Curtis) (Borcard *et al*. 2018).

Table 1. Maturation stages of gametangia in mosses, adapted from Stark (2002).

Phenophase		Initial Event
Early	1	Gametangium visible at 400x; Sex can be indistinguishable
Immature	2	Gametangium reaching 1/2 length of a mature one
Mature	3	Freshly broken capsule; Hyaline or green gametangium.
Dehiscent	4	Gametangium brownish in color with broken apexes.
Early Embryo	5	Gametangium with zygote or sprouts of sporophytes emission
Aborted	A	Gametangium with brownish color with withered appearance

For the phenological study, circular statistics were employed to assess differences in the seasonality of reproductive events between the two areas. This analysis aimed to determine whether there are distinct patterns of reproductive receptivity and temporal separation in reproductive periods between the two locations (Morellato *et al*. 2010). Firstly, the monthly occurrences of phenophases were recorded in absolute numbers for each environment. Afterwards, the months of the year were converted into degrees ranging from 0° to 360° (January as 0° and December as 360°), and the mean vector value (angles), the length of the mean vector to determine the directional consistency of the data, the median (angles), circular standard deviation (CSD) and Rayleigh test (Z and P) to verify the uniformity of the data distribution were calculated (Zar 1999; Morellato *et al*. 2010).

For the morphometric studies, the native GUI for R ver. 3.2.5 (R Core Team 2024) was used with the "vegan" package (Oksanen *et al*. 2024). For the phenological studies, the software "Oriana" ver. 4.02 (Kovach Computing Services 2024) was used.

RESULTS

A total of 4,320 leaves were analyzed, totaling 21,600 measurements of morphometric characters in the gametophytic phase. Multivariate analysis using principal component analysis (PCA) of the five gametophytic morphometric characters among the two environments indicated morphological discontinuities in three of the four focal species: *Leucobryum martianum*, *Octoblepharum pulvinatum* and *Pilosium chlorophyllum* (Figure 3; Supplementary Material, Figure S1). As for *O. albidum*, no significant morphological differences were detected among individuals inhabiting both environments.

When comparing gametophytic characters among environments using the t-test, these three species showed significant differences in more than one or in all morphometric characters analyzed. However, *O. albidum* showed a difference in only one morphometric character: basal length (Table 2). The length-related characters, such as apical, basal and total length, showed the greatest frequencies of significant difference among the two habitats; however, the hypothesized trend of

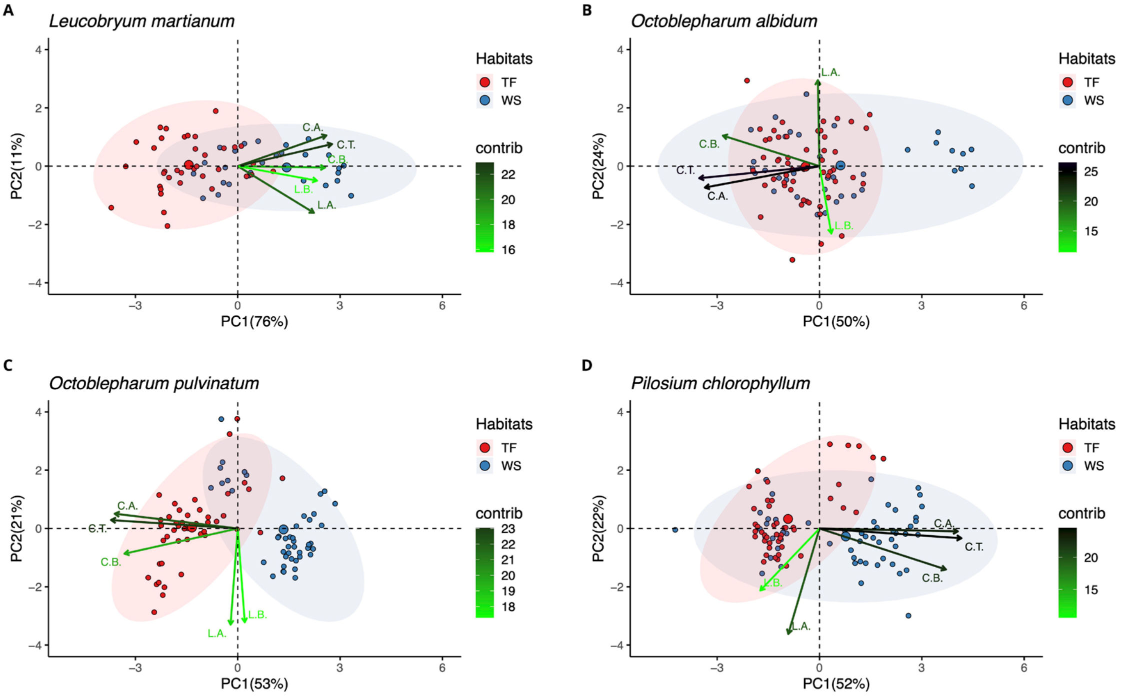

Figure 3. Principal component analysis (PCA) of phenotypic variation in gametophytic characters for four bryophyte species: *Leucobryum martianum* (**A**), *Octoblepharum albidum* (**B**), *Octoblepharum pulvinatum* (**C**), and *Pilosium chlorophyllum* (**D**), across terra-firme (TF, triangles) and campinarana (WS, circles) habitats. Percentages indicate the variance explained by Principal Component 1 (PC1) and Principal Component 2 (PC2). Variable contributions (contrib) are proportional to their influence on the axes, with higher values denoting greater importance. Abbreviated phenotypic traits correspond to specific morphological characters analyzed (L.A = apical width, L.B = basal width, C.B = basal length, C.A = apical length, C.T = the total length taken across the sum of AW and BW.

Table 2. Morphometric comparison between specimens from Terra-firme and Campinaranas (W-S). Values are mean measurements in µm. AL = Apical length; BL = Basal length; TL = Total length; AW = Apical width; BW = Basal width; t-value = t-test value; p-value = Probability value; N.S. = not significant (P>0.05).

Variable	W-S	Terra-Firme	t-value	p-value
		Leucobryum martianum		
AL	465.50	324.40	7.92	<0.001
BL	114.10	52.50	6.74	<0.001
TL	578.60	377.00	8.52	<0.001
AW	40.83	24.47	6.71	<0.001
BW	70.58	48.08	5.84	<0.001
		Octoblepharum albidum		
AL	356.16	390.31	-1.18	N.S.
BL	75.75	100.20	-3.30	<0.001
TL	431.91	490.51	-1.80	N.S.
AW	36.22	35.98	0.10	N.S.
BW	53.55	55.79	-0.69	N.S.
		Octoblepharum pulvinatum		
AL	164.60	432.40	-11.60	<0.001
BL	41.15	104.00	-9.13	<0.001
TL	205.75	536.40	-12.53	<0.001
AW	36.91	37.31	-0.18	N.S.
BW	58.51	57.20	0.35	N.S.
		Pilosium chlorophyllum		
AL	296.81	156.80	5.15	<0.001
BL	87.55	41.57	7.90	<0.001
TL	384.37	198.37	5.84	<0.001
AW	39.22	35.64	1.53	N.S.
BW	56.70	6.60	-1.60	N.S.

generally reduced leaf surface area for white-sands forests was not reflected in the results (Table 2). In fact, high inter-specific variability was documented among the phenotypic trends for leaf characteristics among the four study species.

For three of the species, *L. martianum, O. pulvinatum and P. chlorophyllum,* positive results from the Mantel test suggest that the differences found were correlated with geographic distance between populations (Figure 4).

Phenology

A total of 4,800 gametophytes were analyzed and 19,862 archegonia, 21,244 antheridia and 308 sporophytes were observed during the study period. Sexual expression was reported for all species in both habitats as either antheridia (male gametangia), archegonia (female gametangia) and/or sporophytes. White-sands specimens showed the highest rates of sexual expression when compared with their upland peers. For both environments, *P. chlorophyllum* had the highest percentages of sexual expression, and *L. martianum* showed the lowest (Figure 5A).

Interestingly, gametangial frequencies observed in populations in both environments showed strong inter-specific variation with multiple cases of strong male bias em sex expression. For example, the sex ratio (SR = antheridia/archegonia) was nearly 2.5x higher (mean SR: 2.24) for males of *L. martinanum* in white-sands habitats, and more than 6x higher for males of *O. albidum* in upland forests. Nonetheless,

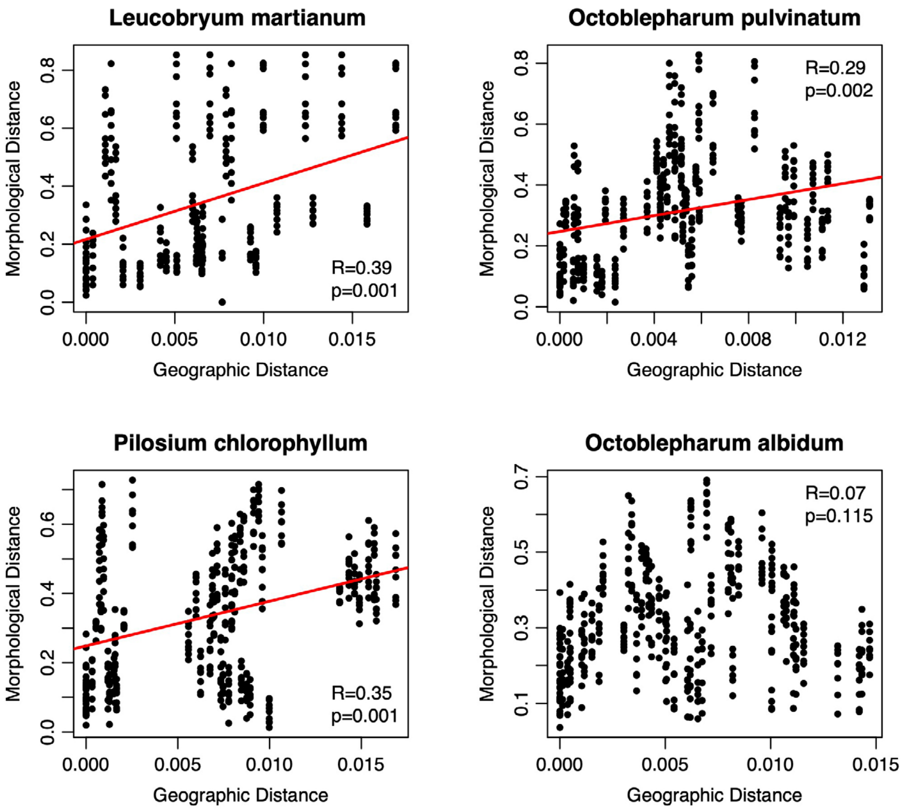

Figure 4. Mantel Test of morphometric variation of the four studied bryophyte species related to the geographical distance (km).

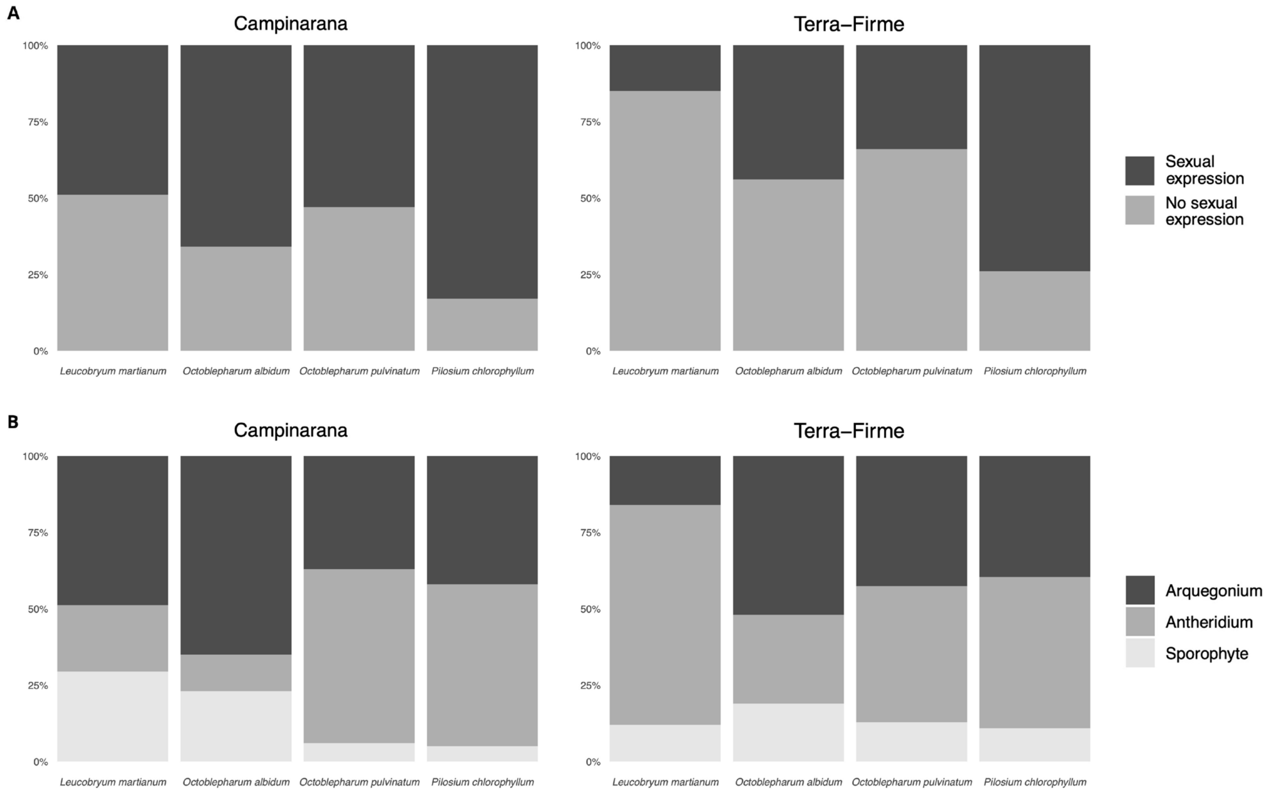

Figure 5. Relative percentage of sexual expression (**A**) and relative percentage of antheridial (♂) / archegonial (♀) expression / sporophyte output (**B**) for the four species.

interspecific variation in SR among white-sands populations was observed as *L. martianum* and *O. albidum* showed high percentages of antheridia expression, while *O. pulvinatum* and *P. chlorophyllum* expressed proportionally greater archegonial expression (Figure 5B, Table 3). Furthermore, substantial intraspecific variation in SR among the two habitats was also observed across all species suggesting the influence of local environment on sex expression.

Only phenophases 3 (gametangia hyaline or green), 4 (gametangia brownish with broken apices), 5 (gametangia with zygote or sporophyte buds) and aborted (gametangia brownish and withered) were observed in the study (Figure 6; Supplementary Material, Table S1, Table S2). The four bryophyte species studied presented distinct seasonal patterns for the phenophases of both antheridia and archegonia among habitats, associated with rainfall seasonality (Figure

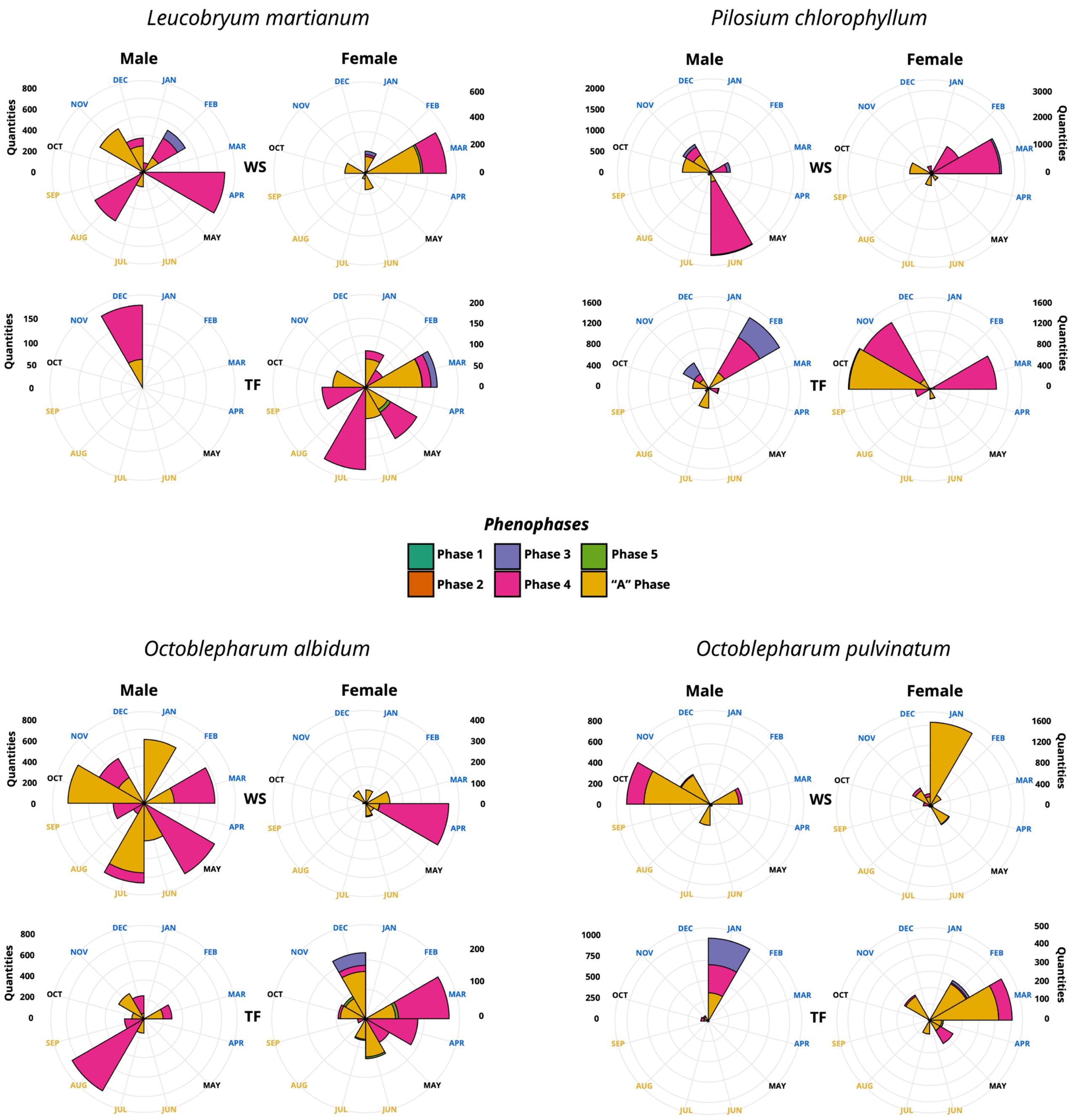

Figure 6. Circular histogram of *Leucobryum martianum*, *Pilosium chlorophyllum*, *Octoblepharum albidum* and *O. pulvinatum* showing the frequency of phenophases observed in white-sands and upland habitats.

Table 3. Summary of sexually expressing gametophytes obtained from 600 gametophytes per species, per habitat type. The sex ratio (SR) was calculated as the total antheridia divided by total archegonia (see Stark *et al.* 2010).

Species	Habitat	Gametophytes with archegonium♀	Gametophytes with antheridia ♂	Total ♀	Total ♂	SR
L. martianum	W-S	90 (15%)	203(34%)	1441	3222	2.24
	Terra-Firme	73 (12%)	16 (3%)	1094	193	0.18
O. albidum	W-S	61 (10%)	334(56%)	870	5439	6.25
	Terra-Firme	93 (16%)	168(28%)	1200	2155	1.80
O. pulvinatum	W-S	190 (32%)	125 (21%)	3239	1724	0.53
	Terra-Firme	105 (18%)	100(17%)	1307	1201	0.92
P. chlorophyllum	W-S	277 (46%)	219 (37%)	5557	4069	0.73
	Terra-Firme	245 (41%)	196 (33%)	5154	3241	0.63

6; Supplementary Material, Table S1, Table S2). Sexual expression in white-sands forests was temporally restricted more so than those of upland forests. Furthermore, aborted archegonia were observed significantly more frequently in the rainy season in white-sands forests.

Curiously, *P. chlorophyllum* was observed in dehiscence (phenophase 4) with greater frequency in the dry season, especially in white-sands forest. Regarding its archegonia, phenophases 3 and 4 were observed within both environments during the rainy season, while phenophase 5 during the dry season. The frequency of abortive phenophase observations among habitats was best represented in white-sands during the dry season, and upland forests during wet months.

For both antheridia and archegonia, the post-antherozoid maturation and post-oosphere receptivity of the dehiscent and abortive phases occurred throughout the entire collection cycle. Curiously however, during the rainy season of November/2016 to May/2017 a low occurrence of the mature phase was reported for both males and females. Circular analyses (Figure 6; Supplementary Material, Table S1, Table S2) revealed a seasonality only for the appearance of female gametangia during the post-maturation phase, for both environments.

DISCUSSION

To our knowledge, no studies of Amazonian cryptogams have yet to address the role of habitat differentiation on phenotypic and phenological variation. Considering that the Amazon is an epicenter for the evolution of neotropical plants (Antonelli *et al.* 2018), understanding patterns of inter-specific variation in reproductive phenology and phenotypic divergences is fundamental for revealing the contributions of Amazonian habitat differentiation to plant speciation processes. Our study reveals substantial infra-specific phenotypic variation among photosynthetically active characters in moss gametophytes, as well as phenological variation in the temporal expression of male and female gametangia among the two habitats. Furthermore, our observations of sex ratio expression reveal an atypically pervasive male bias for three of the four study species among all populations independent of habitat type.

White-sands and Terra-firme plateaus are characterized by different edaphic and microclimatic conditions. That is, white-sands are typically drier and subject to greater solar radiation due to the reduced density in canopy tree architecture and sandier soil types (Adeney *et al.* 2016; Fine and Baraloto 2016). Bryophytes, dependent on the presence of water for successful fertilization, are generally temporally restricted in sexual expression in drier micro-climates. Indeed, all four species in both environments displayed opportunistic strategies as gametangial production was frequent, thus allowing for the convergence of reproduction and gamete maturation with local water availability. In general, our phenological analysis reveals temporal restrictions in sexual expression particularly in males among white-sands populations. However, interspecific variation was observed as best illustrated in the case of *L. martianum* with unexpectedly high sexual expression during the dry season for populations inhabiting both habitats.

The biology of tropical bryophytes remains understudied; however evidence suggests that they employ a diverse array of reproductive strategies with characteristically high phenotypic variation within and among populations (Maciel-Silva *et al.* 2011; Pereira *et al.* 2013; Laenen *et al.* 2016; Silva *et al.* 2017; dos Santos *et al.* 2020). Such factors putatively contribute to their potential fitness advantages as best illustrated by their greater ecological amplitude when compared to Amazonian phanerogams (*pers. obs.* CEZ). Curiously, in our study however the ecological generalist and cosmopolitan species *Octoblepharum albidum* (Santos & Stech 2016) revealed less phenotypic variation than the other three species suggesting that for this species habitat heterogeneity is not the principal factor driving population divergence. Nonetheless, similar studies at regional spatial scales are necessary to test this hypothesis.

Leaf traits, such as surface area, typically respond to environmental exposure such as light and water resources, which when adequate result in the resource reallocation to other life history aspects such as growth and reproduction (Andrade *et al.* 2013; Taiz *et al.* 2017; Glime 2021). Although significant morphometric divergences were observed among the measured traits for all four focal species, the direction of these changes among habitat types was not consistent among species. Contrary to our hypothesis, that leaf surface area would diminish in white-sands habitats relative to terra-firme plateaus, no common trend across species was documented. In fact, phenotypes were mixed and complex with no established pattern among habitats and species. In summary, high observed phenotypic variation was not related to identifiable aspects of habitat differences.

Finally, and perhaps most surprisingly was the discovery of highly lopsided sex ratios towards male expression. Much interest has been dedicated to the nearly ubiquitous observation of female expression dominating bryophyte populations globally: a phenomenon coined the shy-male hypothesis (Stark *et al.* 2010). Interpretations of this anomalous reproductive behaviour (i.e., male expression generally more common among flowering plants (Barrett *et al.* 2010) point to the possibility that resource allocation, contrary to phanerogams, is relatively higher for male expression in bryophytes thus resulting in sex ratios (SR) skewed to female expression. Interestingly, our results show SR contrary to the historical pattern of female dominated expression documented for temperate species. A possible explanation may lie in the strong seasonality in rainfall which typically comes in tropical deluges reducing antherozoid densities in short episodes of heavy rainfall. Aquatic bryophytes adapted to a similar ecological challenge by allocating resources to male expression to augment antherozoid densities to compensate for water volume (Shevock *et al.* 2017). Whether reproductive strategies of terrestrial Amazonian bryophytes have converged with rheophytic species due to similar ecological pressures remains to be tested.

CONCLUSIONS

Our findings provide clues into the evolutionary potential of Amazonian bryophytes as we show that these four common neotropical bryophytes exhibit substantial phenotypic and phenological variation at the meso-scale in two common habitats. The unexpectedly high rate of male expression is noteworthy as such a reproductive strategy is globally uncommon among bryophytes. Future studies should aim to gather data across greater spatial scales to deepen our understanding of the mechanisms that drive survival, maintenance, reproduction and speciation of bryophytes in tropical environments.

ACKNOWLEDGMENTS

This research was funded by a master's scholarship from the Brazilian *Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior* (CAPES-DS/MEC), given to AKNCS. We thank the Botany Graduate Program at the *Instituto Nacional de Pesquisas da Amazônia* (PPG-BOT/INPA), *Instituto Chico Mendes de Conservação da Biodiversidade* (ICMBio) and Natura for the logistical, financial and institutional support. TAJ was partially supported by a master's scholarship given by the Fundação de Amparo à Pesquisa do Estado do Amazonas (POSGRAD/FAPEAM) during the writing of this manuscript.

REFERENCES

Adeney, J.M.; Christensen, N.; Vicentini, A.; Cohn-Haft, M. 2016. White-sand ecosystems in Amazonia. *Biotropica* 48: 7-23.

Allen, N.S. 1992. Notas para la revisión de las especies de *Octoblepharum* del neotrópico. *Tropical Bryology* 6: 171-179.

Andrade, E.A.; Barbosa, M.E.A.; Demetrio, G.R. 2013. Density-dependent morphological plasticity and trade-offs among vegetative traits in *Eichhornia crassipes* (Pontederiaceae). *Acta Amazonica* 43: 455-460.

Antonelli, A.; Zizka, A.; Carvalho, F.A.; Scharn, R.; Bacon, C.D.; Silvestro, D.; Condamine, F.L. 2018. Amazonia is the primary source of Neotropical biodiversity. *Proceedings of the National Academy of Sciences* 115: 6034-6039.

Barrett, S.C.H.; Yakimowski, S.B.; Field, D.L.; Pickup, M. 2010. Ecological genetics of sex ratios in plant populations *Philosophical Transactions of the Royal Society Publishing (B)* 365: 2549–2557.

Baythavong, B.S.; Stanton, M.L. 2010. Characterizing selection on phenotypic plasticity in response to natural environmental heterogeneity. *Evolution* 64: 2904-2920.

Beck, H.E.; Zimmermann, N.E.; McVicar, T.R.; Vergopolan, N.; Berg, A.; Woods, E.F. 2018. Data Descriptor: Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Nature Scientific Data* 5: 180214.

Borcard, D.; Gillet, F.; Legendre, P. 2018. *Numerical Ecology with R*. Springer, Cham. 435p.

Bowker, M.A.; Stark, L.R.; McLetchie, D.N.; Mishler, B.D. 2000. Sex expression, skewed sex ratios, and microhabitat distribution in the dioecious desert moss *Syntrichia caninervis* (Pottiaceae). *American Journal of Botany* 87: 517-526.

Capurucho, J.M.G.; Borges, S.H.; Cornelius, C.; Vicentini, A.; Prata, E.M.B.; Costa, F.M.; *et al.* 2020. Patterns and Processes of Diversification in Amazonian White Sand Ecosystems: Insights from Birds and Plants. In: Rull, V.; Carnaval, A.C. (Eds.). *Neotropical Diversification: Patterns and Processes*. SpringerLink, Switzerland. p.245-270.

Cardoso, D.; Särkinen, T.; Alexander, S.; Forzza, R.C. 2017. (…) por Cardoso, D.; Särkinen, T.; Alexander, S.; Amorim,A.M.; Bittrich, V.; Celis, M.; et al. 2017. Amazon plant diversity revealed by a taxonomically verified species list. *Proceedings of the National Academy of Science* 114: 10695-10700.

Cerqueira, G.R.; Sierra, A.M.; Ilkiu-Borges, A.L.; Mota-de-Oliveira, S; Zartman, C.E. 2021. Unveiled diversity: Amazonian Campinaranas harbor twice the number of bryophyte species recorded in the last century. *Acta Botanica Brasilica* 35: 418-431.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure.Australian Journal of Ecology 18: 117-143.

Costa, D.P.; Peralta, D.F. 2015. Bryophytes diversity in Brazil. *Rodriguésia* 66: 1063-1071.

Costa, D.P.; Nadal, F.; Rocha, T.C. 2020. The first botanical explorations of bryophyte diversity in the Brazilian Amazon mountains: high species diversity, low endemism, and low similarity. *Biodiversity and Conservation* 29: 2663-2688.

Coyne, J.A.; Orr, H.A. 2004. *Speciation*. Sinauer Associates, Sunderland. 545p.

Demarchi, L.O.; Klein, V.P.; Aguiar, D.P.P.; Marinho, L.C.; Ferreira, M.J. Lopes, A.; *et al.* 2021. The specialized white-sand flora of the Uatumã Sustainable Development Reserve, central Amazon, Brazil. *CheckList* 18: 187-217.

dos Santos, W.L.; Maciel-Silva, A.S.; Pôrto, K.C. 2020. How do sexual expression, reproductive phenology and reproductive success relate to sexual systems in *Fissidens* Hedw. (Fissidentaceae)? A case study comparing two different sexual systems in mosses. *Plant Biology* 22: 573-581.

Fischer, K.M.; Wall, D.P.; Yip, K.L. Mishler, B.D. 2007. Phylogeny of the Calymperaceae with a rank-free systematic treatment. *The Bryologist* 110: 46-73.

Fine, P.V.A. 2015. Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution and Systematics* 45: 369-392.

Fine, P.V.A.; Baraloto, C. 2016. Habitat endemism in white-sand forests: Insights into the mechanisms of lineage diversification and community assembly of the Neotropical flora. *Biotropica* 48: 24-33.

Glime, J. 2021. Bryophyte Ecology. https://digitalcommons.mtu.edu/oabooks/4

Gradstein, S.R. 1992. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J.W.; Farmer, A.M. (Eds). *Bryophytes and lichens in a Changing Environment*. Claredon Press, Oxford. p.232-256.

Gradstein, S.R.; Churchill, S.P.; Salazar-Allen, N. 2001. *Guide to the Bryophytes of Tropical America*. NYBG Press, New York. 577p.

Greene, S.W. 1960. The maturation cycle, or the stages of development of gametangia and capsules in mosses. *Transactions of the British Bryological Society* 3: 736-745.

INMET. 2018. Instituto Nacional de Meteorologia. Dados Históricos Anuais. Brasília.(https://portal.inmet.gov.br/dadoshistoricos). Accessed on 02/08/2024.

Jägerbrand, A.K.; Jonsdottir, I.S.; Økland, R.H. 2005. Phenotypic variation at different spatial scales in relation to environment in two circumpolar bryophyte species. *Lindbergia* 30: 125-142.

Komura, D.L.; Wartchow, F.; Cabral, T.S. 2021. *Pseudotulostoma volvatum* (Elaphomycetaceae, Ascomycota) from an Amazonian white-sand forest in Brazil: odd and rare in the Neotropics? *Plant Systematics and Evolution* 307: 65.

Kovach Computing Services. 2024. Oriana - circular statistics, circular data, rose diagrams.(https://www.kovcomp.co.uk/oriana/).

Laaka-Lindberg, S. 2005. Reproductive phenology in the leafy hepatic *Lophozia silvicola* Buch in southern Finland. *Journal of Bryology* 27: 253-9

Laenen, B.; Machas, A.; Gradstein, S.R.; Shaw, B.; Patiño, J.; Desamore, A.; *et al.* 2016. Geographical range in liverworts: Does sex really matter? *Journal of Biogeography* 43: 627-635.

Lewinsohn, T.M.; Prado, P.I. 2005. Quantas espécies há no Brasil? *Megadiversidade* 1: 36-42.

Luna, E.; Velasco, G.G. 2008. Morphometrics and the Identification of *Braunia andrieuxii* and *B. secunda* (Hedwigiaceae, Bryopsida). *Systematic Botany* 33: 219-228.

Maciel-Silva, A.S.; Válio, I.F.M. 2011. Reproductive phenology of bryophytes in tropical rain forests: the sexes never sleep. *Bryologist* 114: 708-719.

Maciel-Silva, A.S.; Válio, I.F.M.; Rydin, H. 2012. Altitude affects the reproductive performance in monoicous and dioicous bryophytes: examples from a Brazilian Atlantic rainforest. *AoB PLANTS* pls016: 1-14

Maciel-Silva, A.S.; Coelho, M.L.P.; Pôrto, K.C. 2013. Reproductive traits in the tropical moss *Octoblepharum albidum* Hedw. differ between rainforest and coastal sites. *Journal of Bryology* 35: 206-215.

Mallet, J.; Meyer, A.; Nosil, P.; Feder, J.L. 2009. Space, sympatry and speciation. *Journal of Evolutionary Biology* 22: 2332-2341.

Mandl, N.A.; Kessler, M.; Gradstein, S.M. 2009. Effects of environmental heterogeneity on species diversity and composition of terrestrial bryophyte assemblages in tropical montane forests of southern Ecuador. *Plant Ecology & Diversity* 2: 313–321.

Morellato, L.P.C.; Alberti, L.F.; Hudson, I.L. 2010. Applications of Circular Statistics in PlantPhenology: a Case Studies Approach. In: Hudson, I.; Keatley, M. (Eds). Phenological Research. Springer, Dordrecht. p. 339-359.

Oksanen, J.; Simpson, G.L.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R. *et al.* 2024. *Vegan: community ecology package*. R Package version 2.2-1. (http://CRAN.R-project.org/package=vegan).

Oliveira, S.M.; ter Steege, H. 2015. Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. *Journal of Ecology* 103: 441-450.

Oliveira-da-Silva, F.R.; Ilkiu-Borges, A.L. 2016. Flora das Cangas da Serra dos Carajás, Pará, Brasil: Stereophyllaceae. *Rodriguésia* 67: 1137-1140.

Pélabon, C.; Osler, N.C.; Diekmann, M.; Graae. B.J. 2013. Decoupled phenotypic variation between floral and vegetative traits: distinguishing between developmental and environmental correlations. *Annals of Botany* 111: 935-944.

Pereira, M.R.; Dambros, C.S.; Zartman, C.E. 2013. Prezygotic resource-allocation dynamics and reproductive trade-offs in Calymperaceae (Bryophyta), *American Journal of Botany* 103: 1838-1846

Perigolo, N.A.; Medeiros, M.B.; Simon, M.F. 2017. Vegetation types of the upper Madeira River in Rondônia, Brazil. *Brittonia* 69: 423-446.

Pires, J.M.; Prance, G.T. 1985. The vegetation types of the Brazilian Amazon. In: Prance, G.T.; Lovejoy, T.E. (Eds.). *Key Environments: AMAZONIA*. Pergamon Press, Oxford. p.109–145.

Pócs, T. 1982. Tropical Forest Bryophytes. In: Smith, A.J.E. (ed.). *Bryophyte Ecology*. Chapter 3. Chapman and Hall, London. p.59-104.

Resende, A.F.; Schöngart, J.; Streher, A.S.; Ferreira-Ferreira, J.; Piedade, M.T.F.; Silva, T.S.F. 2019. Massive tree mortality from flood pulse disturbances in Amazonian floodplain forests: The collateral effects of hydropower production. *Science of the Total Environment* 659: 587-598.

Rousk, K.; Villarreal, A.J.C. 2024. Time to end the vascular plant chauvinism. *Nature Plants*. https://doi.org/10.1038/s41477-024-01876-9.

Santos, M.B.; Stech, M. 2016. Tackling relationships and species circumscriptions of *Octoblepharum*, an enigmatic genus of haplolepideous mosses (Dicranidae, Bryophyta). *Systematics and Biodiversity* 15: 16–24.

Shevock, Ma, W-Z.; Akiyama, H. 2017. Diversity of the rheophytic condition in bryophytes: field observations from multiple continents. *Bryophyte Diversity and Evolution* 39: 75.

Silva, A.K.N.C.; Dambros, C.S.; Pereira, M.R.; Zartman, C.E. 2017. Is phenotypic variation reflected in habitat connectivity? A morphometric comparison of two moss species from insular and continuous habitats of the Amazon Basin. *Bryophyte Diversity and Evolution* 39: 102-114.

Sierra, A.M.; Vanderpooten, A.; Gradstein, S.R.; Pereira, M.R.; Bastos, C.J.P.; Zartman, C.E. 2018. Bryophytes of Jaú National Park (Amazonas, Brazil): Estimating species detectability and richness in a lowland Amazonian megareserve. *The Bryologist* 121:571-588.

Stark, L.R. 2002. Phenology and Its Repercussions on the Reproductive Ecology of Mosses. *The Bryologist* 105: 204-218.

Stark, L.R.; McLetchie, D.N.; Eppley, S.M. 2010. Sex ratios and the shy male hypothesis in the moss *Bryum argenteum* (Bryaceae). *The Bryologist* 113: 788-797.

Stiling, P.D. 2002. *Ecology: Theories e Applications*. Prentice Hall, London. 403p.

Vanderpoorten, A.; Goffinet, B. 2009. *Introduction of Bryophytes*. Cambridge University Press, Cambridge. 294p.

Taiz, L.; Zeiger, E.; Moller, I.M.; Murphy, A. 2017. *Fisiologia e Desenvolvimento Vegetal, 6ª ed*. Artmed, Porto Alegre. 858p.

ter Steege, H.; Pitman, N.C.A.; Philips, O.L.; Chave, J.; Sabatier, D.; Duque, A.; *et al*. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443: 444-447.

ter Steege, H.; Vaessen, R.W.; Cárdenas-López, D.; Sabatier, D.; Antonelli, A.; Oliveira, S.M.; *et al*. 2016. The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. *Scientific Reports* 6: 29549.

Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River.

Zartman, C.E.; Amaral, J.A.; Figueiredo, J.N.; Dambros, C.S. 2015. Drought impacts survivorship and reproductive strategies of an epiphyllous leafy liverwort in Central Amazonia. *Biotropica* 47: 172-178.

RECEIVED: 15/08/2024
ACCEPTED: 04/02/2025
ASSOCIATE EDITOR: Carolina Castilho

DATA AVAILABILITY: The data that support the findings of this study were published in this article in the "Supplementary Material".

SUPPLEMENTARY MATERIAL

Silva *et al*. Exploring local phenological and phenotypic variation of mosses (Bryophyta) in two common Amazonian habitats

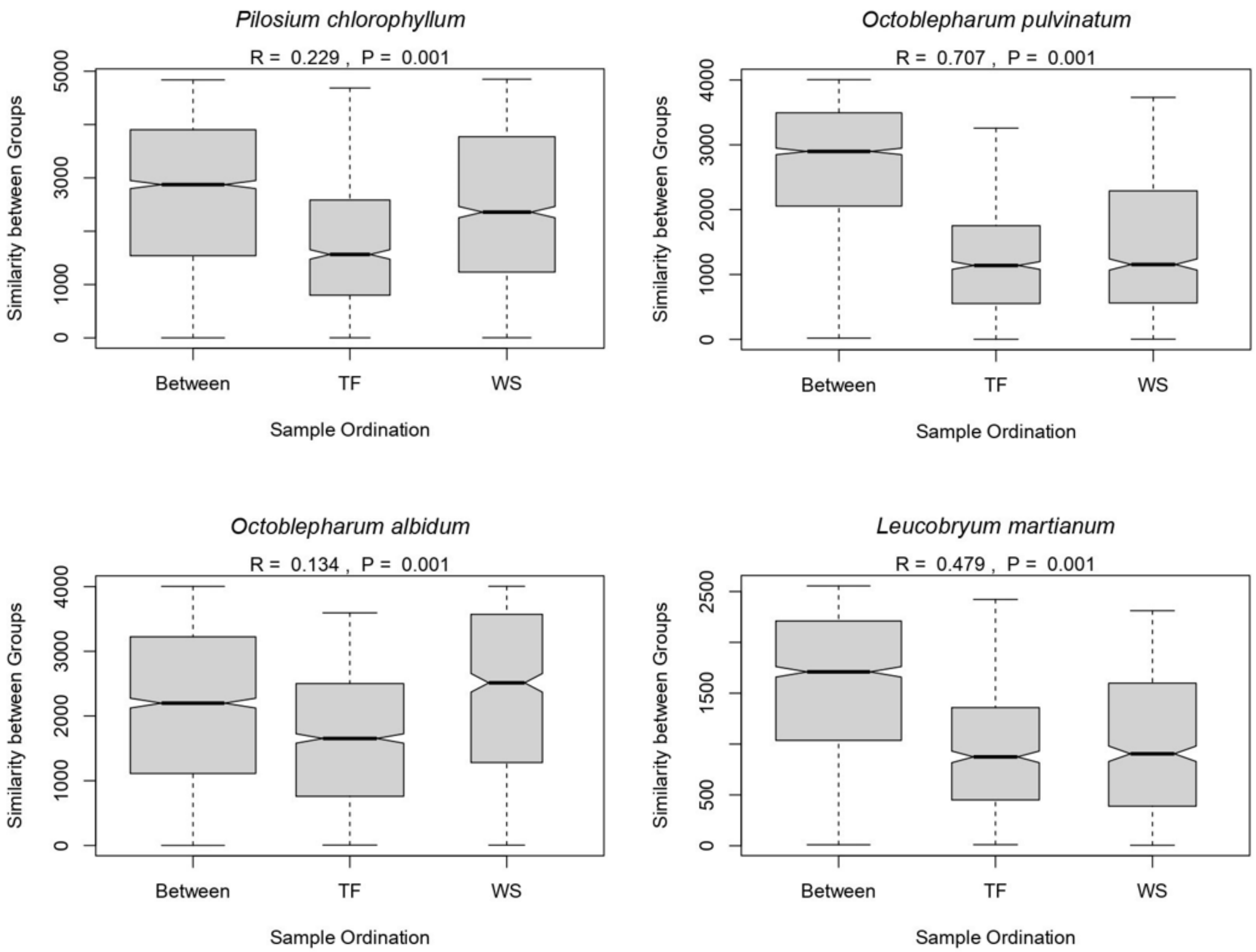

Figure S1. Analysis of Similarity (ANOSIM) Results

Table S1. Results of the circular statistical analyses, female individuals.

	Variables	Phases					
		Phase 1	Phase 2	Phase 3	Phase 4	Phase 5	Aborted
	Leucobryum martianum - FEMALE						
Campinaranas	Observations (n)	0	0	0	262	19	1129
	Mean Month	*****	*****	*****	Feb	Mar	Mar
	Mean Vector (α)	*****	*****	*****	54,122°	60°	67,772°
	Length of mean vector (r)	*****	*****	*****	0,96	1	0,39
	Median	*****	*****	*****	60°	60°	75°
	Circular Standard Deviation (SD)	*****	*****	*****	84,787°	*****	78,327°
	Rayleigh Test (Z)	*****	*****	*****	240,10	19	174,20
	Rayleigh test of uniformity (P)	*****	*****	*****	<0,001	<0,001	<0,001
Terra-firme	Observations (n)	0	0	18	558	12	506
	Mean Month	*****	*****	Apr	Jun	May	Mar
	Mean Vector (α)	*****	*****	90°	176,011°	120°	87,896°
	Length of mean vector (r)	*****	*****	1	0,47	0,833	0,33
	Median	*****	*****	90°	180°	120°	75°
	Circular Standard Deviation (SD)	*****	*****	*****	70,762°	34,598°	85,602°
	Rayleigh Test (Z)	*****	*****	18	121,40	8,333	54,29
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001	<0,001	<0,001
	Octoblepharum albidum - FEMALE						
Campinaranas	Observations (n)	0	0	0	373	15	490
	Mean Month	*****	*****	*****	Apr	Aug	Mar
	Mean Vector (α)	*****	*****	*****	90°	218,948°	61,653°
	Length of mean vector (r)	*****	*****	*****	1	0,37	0,41
	Median	*****	*****	*****	90°	270°	60°
	Circular Standard Deviation (SD)	*****	*****	*****	*****	80,665°	76,472°
	Rayleigh Test (Z)	*****	*****	*****	373	2,067	82,518
	Rayleigh test of uniformity (P)	*****	*****	*****	<0,001	0,126	<0,001
Terra-firme	Observations (n)	0	0	43	501	28	628
	Mean Month	*****	*****	Dec	Mar	Aug	Nov
	Mean Vector (α)	*****	*****	330°	83,109°	92,374°	300,129°
	Length of mean vector (r)	*****	*****	1	0,74	0,17	0,15
	Median	*****	*****	330°	90°	60°	300°
	Circular Standard Deviation (SD)	*****	*****	*****	44,953°	108,014°	111,566°
	Rayleigh Test (Z)	*****	*****	43	270,71	0,80	14,17
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001	0,453	<0,001

Table S1. Continued.

	Variables	Phases					
		Phase 1	**Phase 2**	**Phase 3**	**Phase 4**	**Phase 5**	**Aborted**
Octoblepharum pulvinatum - FEMALE							
Campinaranas	Observations (n)	0	0	0	289	0	2936
	Mean Month	*****	*****	*****	Oct	*****	Jan
	Mean Vector (α)	*****	*****	*****	284,955°	*****	4,562°
	Length of mean vector (r)	*****	*****	*****	0,89	*****	0,67
	Median	*****	*****	*****	270°	*****	0°
	Circular Standard Deviation (SD)	*****	*****	*****	28,161°	*****	51,125°
	Rayleigh Test (Z)	*****	*****	*****	226,98	*****	315,61
	Rayleigh test of uniformity (P)	*****	*****	*****	<0,001	*****	<0,001
Terra-firme	Observations (n)	0	0	326	191	0	1079
	Mean Month	*****	*****	Feb	Mar	*****	Mar
	Mean Vector (α)	*****	*****	30°	86,677°	*****	50,804°
	Length of mean vector (r)	*****	*****	1	0,76	*****	0,581
	Median	*****	*****	30°	60°	*****	60°
	Circular Standard Deviation (SD)	*****	*****	*****	42,317°	*****	59,726°
	Rayleigh Test (Z)	*****	*****	16	110,70	*****	364,01
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001	*****	<0,001
Pilosium chlorophyllum - FEMALE							
Campinaranas	Observations (n)	0	0	76	3767	3	1727
	Mean Month	*****	*****	Feb	Jan	May	Aug
	Mean Vector (α)	*****	*****	51,555°	17,412°	120°	236,771°
	Length of mean vector (r)	*****	*****	0,93	0,94	1,00	0,37
	Median	*****	*****	60°	30°	120°	270°
	Circular Standard Deviation (SD)	*****	*****	21,642°	19,887°	*****	81,372°
	Rayleigh Test (Z)	*****	*****	65,9	3339,4	3,0	229,8
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001	0,033	<0,001
Terra-firme	Observations (n)	0	0	16	2913	18	229
	Mean Month	*****	*****	Oct	Jan	Jun	Oct
	Mean Vector (α)	*****	*****	270°	344,169°	158,66°	273,355°
	Length of mean vector (r)	*****	*****	1,00	0,41	0,71	0,75
	Median	*****	*****	270°	300°	120°	270°
	Circular Standard Deviation (SD)	*****	*****	*****	76,195°	47,278°	43,466°
	Rayleigh Test (Z)	*****	*****	65,9	496,9	9,1	1290,7
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001	<0,001	<0,001

Table S2. Results of the circular statistical analyses, male individuals.

	Variables	Phases			
		Phase 1	Phase 2	Phase 3	Phase 4
	Leucobryum martianum - MALE				
Campinaranas	Observations (n)	0	0	97	3125
	Mean Month	*****	*****	Feb	Jan
	Mean Vector (α)	*****	*****	30°	16,631°
	Length of mean vector (r)	*****	*****	1	0,118
	Median	*****	*****	30°	330°
	Circular Standard Deviation (SD)	*****	*****	*****	118,409°
	Rayleigh Test (Z)	*****	*****	97	43,651
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001
Terra-firme	Observations (n)	0	0	0	193
	Mean Month	*****	*****	*****	Dec
	Mean Vector (α)	*****	*****	*****	330°
	Length of mean vector (r)	*****	*****	*****	1
	Median	*****	*****	*****	330°
	Circular Standard Deviation (SD)	*****	*****	*****	*****
	Rayleigh Test (Z)	*****	*****	*****	193
	Rayleigh test of uniformity (P)	*****	*****	*****	<0,001
	Octoblepharum albidum - MALE				
Campinaranas	Observations (n)	0	0	0	5439
	Mean Month				Jul
	Mean Vector (α)	*****	*****	*****	183,417°
	Length of mean vector (r)	*****	*****	*****	0,107
	Median	*****	*****	*****	150°
	Circular Standard Deviation (SD)	*****	*****	*****	121,089°
	Rayleigh Test (Z)	*****	*****	*****	62,482
	Rayleigh test of uniformity (P)	*****	*****	*****	<0,001
Terra-firme	Observations (n)	0	0	0	2155
	Mean Month	*****	*****	*****	Sep
	Mean Vector (α)	*****	*****	*****	240,37°
	Length of mean vector (r)	*****	*****	*****	0,457
	Median	*****	*****	*****	210°
	Circular Standard Deviation (SD)	*****	*****	*****	71,662°
	Rayleigh Test (Z)	*****	*****	*****	450,884
	Rayleigh test of uniformity (P)	*****	*****	*****	<0,001

	Variables	Phases			
		Phase 1	Phase 2	Phase 3	Phase 4
	Octoblepharum pulvinatum - MALE				
Campinaranas	Observations (n)	0	0	0	1724
	Mean Month	*****	*****	*****	Oct
	Mean Vector (α)	*****	*****	*****	277,462°
	Length of mean vector (r)	*****	*****	*****	0,482
	Median	*****	*****	*****	270°
	Circular Standard Deviation (SD)	*****	*****	*****	69,187°
	Rayleigh Test (Z)	*****	*****	*****	401,116
	Rayleigh test of uniformity (P)	*****	*****	*****	<0,001
Terra-firme	Observations (n)	0	0	326	875
	Mean Month	*****	*****	Jan	Jan
	Mean Vector (α)	*****	*****	0°	347,995°
	Length of mean vector (r)	*****	*****	1	0,866
	Median	*****	*****	0°	0°
	Circular Standard Deviation (SD)	*****	*****	*****	30,77°
	Rayleigh Test (Z)	*****	*****	326	655,768
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001
	Pilosium chlorophyllum - MALE				
Campinaranas	Observations (n)	0	0	178	3891
	Mean Month	*****	*****	Jan	Jun
	Mean Vector (α)	*****	*****	18,225°	180,04°
	Length of mean vector (r)	*****	*****	0,37	0,314
	Median	*****	*****	60°	150°
	Circular Standard Deviation (SD)	*****	*****	80,478°	87,238°
	Rayleigh Test (Z)	*****	*****	24,75	383,036
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001
Terra-firme	Observations (n)	0	0	716	2525
	Mean Month	*****	*****	Jan	Jan
	Mean Vector (α)	*****	*****	2,037°	12,377°
	Length of mean vector (r)	*****	*****	0,72	0,3
	Median	*****	*****	30°	30°
	Circular Standard Deviation (SD)	*****	*****	46,183°	88,864°
	Rayleigh Test (Z)	*****	*****	373,89	227,805
	Rayleigh test of uniformity (P)	*****	*****	<0,001	<0,001