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MARÍA ALEJANDRA BUITRAGO ARISTIZÁBAL

GEOGRAPHICAL STRUCTURE OF MORPHOLOGY AND SPECTRAL DIVERSITY IN ARUMÃS (*ISCHNOSIPHON* KÖRN., MARANTACEAE)

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GEOGRAPHICAL STRUCTURE OF MORPHOLOGY AND SPECTRAL DIVERSITY IN ARUMÃS (*ISCHNOSIPHON* KÖRN., MARANTACEAE)

Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade da Universidade Federal do Oeste do Pará como parte dos requisitos para obtenção do título de Mestre em Biodiversidade.

Area de concentração: Sistemática e Evolução.

Orientador: Prof. Dr. Thiago André
Co-orientador: Dr. Fernando Figueiredo

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ATA Nº 2

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Assim, aos trinta e um dias do mês de julho do ano de dois mil e dezenove, às 10h00min, no auditório da Pró-reitoria de Pesquisa, Pós-graduação e Inovação Tecnológica (PROPPIT), instalou-se a apresentação de seminário público da dissertação de mestrado da aluna MARÍA ALEJANDRA BUITRAGO ARISTIZÁBAL. Deu-se início a abertura dos trabalhos, onde o Professor Dr. Thiago José de Carvalho André, após esclarecer as normativas de tramitação da defesa e seminário público, de imediato solicitou à candidata que iniciasse a apresentação da dissertação, intitulada Estrutura geográfica da diversidade morfológica e espectral em arumãs ((ISCHNOSIPHON KÖRN., Marantaceae). Concluída a exposição, o orientador comunicou ao discente que a versão final da dissertação deverá ser entregue ao programa, no prazo de 30 dias; contendo as modificações sugeridas pela banca examinadora e constante nos formulários de avaliação da banca.

A banca examinadora foi composta pelos examinadores professores doutores listados abaixo. Os pareceres assinados seguem em sequência.

Thiagojosé de Carvalho André

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Mestrando

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ABSTRACT

Recognition and delimitation of taxonomic categories of biological organisms are still challenging and full of controversies. Traditional categorization of species may hamper the continuous variation of entities in nature. The assessment of morphometric and spectral variation of individuals along geographical and environmental gradients can be used to understand how homogeneous or grouped is the variation and may underscore the delimitation of natural units. We used *Ischnosiphon* (Marantaceae) as a model due to its great morphological variation and broad distribution. Species of this genus are terrestrial rhizomatous herbs, occurring in the understories of tropical forests from Nicaragua to southern Bolivia and Brazil. Here we apply an individual-based approach to test how variation of 22 wide to narrowly distributed species of *Ischnosiphon* is related to ecological factors and geographical distribution, besides describing morphological and spectral variation patterns. We demonstrate great diversity and morphological complexity among *Ischnosiphon*, and propose a replicable and analytical framework to accommodate individual variability in species diagnosis on morphologically diverse plant groups. Additionally, we show that range size is not a good predictor of phenotypic variance and that climatic distance is often more relevant to morphological and spectral variation than geographic distance. These results provide evidence of how our interpretation and recognition of species is prone to underestimation of the role of individual variability, and how environmental gradients influence phenotypic variation of widely distributed organisms. Finally, we discuss the relevance of phenotypic variability explorations on systematics, evolutionary and ecological studies.

Keywords: Climate, Neotropics,Monocots, morphometrics, phenotype, Zingiberales.

RESUMO

O reconhecimento e a delimitação de categorias taxonômicas de organismos biológicos ainda são desafiadores e cheios de controvérsias. A categorização tradicional de espécies pode esconder a variação contínua das entidades na natureza. A avaliação da variação morfométrica e espectral dos indivíduos ao longo de gradientes geográficos e ambientais pode ser usada para entender o quão homogênea ou agrupada é a variação e pode ressaltar a delimitação de unidades naturais. Utilizamos o gênero *Ischnosiphon* (Marantaceae) como modelo para testar essas ideias devido à grande variação morfológica e sua ampla distribuição geográfica. Espécies deste gênero são ervas rizomatosas terrestres que ocorrem nos sub-bosques de florestas tropicais desde a Nicarágua até o sul da Bolívia e do Brasil. Aqui aplicamos uma abordagem baseada em indivíduos para testar como a variação de 22 espécies de *Ischnosiphon,* de distribuição ampla ou restrita, está relacionada a fatores ecológicos e à distribuição geográfica, além de descrever padrões gerais da variação morfológica e espectral das espécies. Nós demonstramos uma grande diversidade e complexidade morfológica entre as espécies de *Ischnosiphon*, e propusemos uma abordagem metodológica replicável e analítica para acomodar a variabilidade individual no diagnóstico de espécies, especialmente em grupos de plantas morfologicamente diversas. Adicionalmente, mostramos que o tamanho da área de distribuição das espécies não é um bom preditor de variância fenotípica, e que a distância climática é frequentemente mais relevante na variação morfológica e espectral do que a distância geográfica. Esses resultados fornecem evidências de como nossa interpretação e reconhecimento das espécies é propensa a subestimar o papel da variabilidade individual, e como os gradientes ambientais influenciam a variação fenotípica de organismos amplamente distribuídos. Finalmente, discutimos a relevância das explorações de variabilidade fenotípica em estudos de sistemática, evolução e ecologia.

Palavras-chave: Clima, fenótipo, Monocotiledôneas, morfometria, Neotrópicos, Zingiberales.

SUMMARY

INTRODUCTION

The value of individuals to understand nature

To create categories is instinctive for humans. By grouping organisms into taxonomic categories, we try to summarize and organize all the diversity of forms we observe in nature. But are we placing organisms into meaningful groups really existent in nature or just uniting what we are able to see? The former is the ideal scenario, while the latter option could basically be distancing us from reality.

In order to collect as much evidence as possible, scientists gather information about the characteristics of particular organisms (traits) at several levels, from spatial distribution on Earth to morphology and genetics, including field observations, building scientific collections and assessing diverse sorts of information available in global biodiversity databases. Interdisciplinary approaches considering evidence based on biological traits taken from individuals along environmental and geographic gradients may yield deeper insights on our understanding of diversity and improve our ability to propose user-friendly and natural classifications.

In particular, biological traits measured from specimens and already available in scientific collections can be used to determine the similarities and differences between diverse groups of organisms. For instance, morphometrics, i.e. the study of shapes and sizes, allows the quantification of differences at the level of individuals and populations and consequently can be used to observe how climatic and geographic factors affect organisms appearance. Furthermore, another set of leaf traits, which captures its chemical composition, cells structure and internal morphology, can be measured with the use of the Near Infrared Spectroscopy (FT-NIR) technique. This tool captures which kind and how much light plant tissues absorb when irradiated with light of a known wavelength range. Thus, spectral responses are almost like fingerprints of each individual and can also be used to characterize the variability among individuals.

Arumãs (Figure 1) are plants from the genus *Ischnosiphon*, culturally and economically important for several Amazonian indigenous people that use its fibres in the manufacturing of baskets and manioc sifters. These organisms display great morphological variation across the geographical range where they occur. Due to the great morphological diversity among Arumãs, species delimitation has been troublesome. This makes Arumã species an ideal group to study how phenotype reflects the evolutionary path where structural variability came from.

Nowadays, identification of *Ischnosiphon* species continues to be problematic for users, taxonomists and ecologists alike, due mainly to the huge morphological variability under species names; the unlikeliness to perceive categorization criteria and circumscription proposed for many species, and also due to the many habitat and vegetative macro-morphological characters lacking in most specimens that are held in scientific collections.

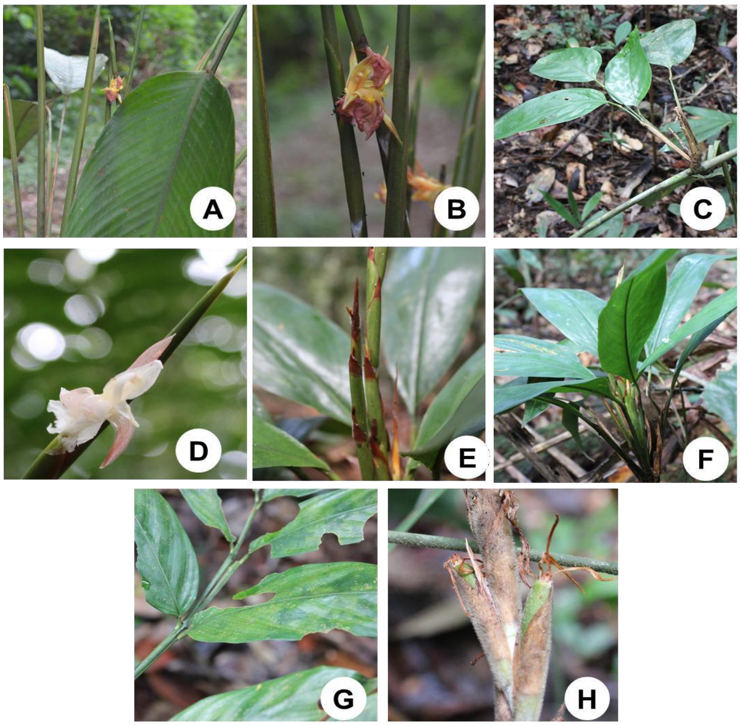

Figure 1. Different species of Arumã, genus *Ischnosiphon* Körn. (A-B) I*schnosiphon obliquus* (Rudge) Körn. Photo by: Thiago André; (C-D) *Ischnosiphon puberulus* Loes.; (E-F) *Ischnosiphon martianus* Eichler ex Petersen; (G-H) *Ischnosiphon crassispicu*s L. Andersson. Photo by: María A. Buitrago.

Morphological traits of plants are available in botanical collections, also known as herbaria, from around the world. These collections are similar to libraries, but instead of books, they preserve whole plants or representative parts of plants that are named specimens.

In this study, the first step after selecting the herbaria material was to obtain morphological and spectral information from each Arumã species. Species are represented in nature by individuals, so it is expected that each specimen represents different or similar forms that a species could have. For this, a total of 60 morphological variables were measured for each of 244 specimens of 22 species using a public platform for scientific image analysis. Likewise, spectral traits were also measured from leaves of specimens deposited at INPA and NY herbaria. Leaf tissues were irradiated directly with the help of a spectrophotometer, and spectral responses were analysed.

The second step consisted of gathering information about the conditions where these plants live. Data about climate (temperature, precipitation, solar radiation, etc.) and geographic coordinates were downloaded from online biodiversity repositories.

The third step was to describe both the morphological and spectral variation of Arumã species, and detect if they were related or not to the environment. Describing the variation of these traits can show if the current classification of Arumãs really takes into account these individual variations. In fact, results of trait variation analyses indicated that Arumã species are much more complex to define if we use only a few morphological traits independently. There are individuals of several species who intermingle, that is, who do not fit in morphological-based categories.

Now, knowing how some Arumã species vary, there are other types of analyses that can reveal if that variation in shape, size and spectral responses is related to the environment. Using these scientific tools we revealed that some Arumãs species are shaped by climatic factors, more precisely by precipitation and temperature. However, most Arumã species show no relation to the variables analysed. It is likely that other factors are influencing observable variation of these plants.

A better understanding of individuals in nature allows the units we use in different areas of science, such as ecology, evolution and systematics, to have a biological sense. We proposed a methodological approach that can be replicated to accommodate individual variability in the identification of species. In addition, it is very important to consider the interaction of individuals with the environment. In Arumãs for example, neither the climate nor spatial distribution were universal predictors of variation of shape, size or spectral responses of the species.

There are many ecological and evolutionary processes in charge of all life forms that we appreciate in the world.

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Suggested readings

Ahrends A, Rahbek C, Bulling MT et al. 2011. Conservation and the botanist effect. Biological Conservation 144: 131–140.

Henderson A. 2006. Traditional morphometrics in plant systematics and its role in palm systematics. Botanical Journal of the Linnean Society 151: 103–111.

Durgante FM, Higuchi N, Almeida A, Vicentini A. 2013. Species Spectral Signature: Discriminating closely related plant species in the Amazon with Near-Infrared Leaf-Spectroscopy. Forest Ecology and Management 209: 240–248.

INTRODUÇÃO

O valor dos indivíduos no entendimento da natureza

Criar categorias é instintivo para os seres humanos. Ao agrupar organismos em categorias taxonômicas, tentamos resumir e organizar toda a diversidade de formas que observamos na natureza. Mas estamos colocando organismos em grupos realmente existentes na natureza ou apenas unindo o que somos capazes de ver? O primeiro é o cenário ideal, enquanto a última opção pode nos distanciar da realidade.

A fim de coletar o máximo possível de evidências, os cientistas coletam informações sobre características de organismos (traços) em vários níveis, desde a distribuição espacial na Terra, até a morfologia e a genética, incluindo observações em campo, construção de coleções científicas e avaliação de diversos tipos de informações disponíveis em bases de dados globais da biodiversidade. Abordagens interdisciplinares, considerando evidências baseadas em características biológicas tiradas de indivíduos ao longo de gradientes ambientais e geográficos, podem fornecer conhecimentos mais profundos sobre nossa compreensão da diversidade e melhorar nossa capacidade de propor classificações fáceis de usar e que reflitam a realidade.

Em particular, características biológicas medidas a partir de espécimes e já disponíveis em coleções científicas podem ser usadas para determinar as semelhanças e diferenças entre diversos grupos de organismos. Por exemplo, a morfometria, isto é, o estudo das formas e tamanhos, permite medir as diferenças no nível de indivíduos e populações e, consequentemente, pode ser usada para observar como os fatores climáticos e geográficos afetam a aparência dos organismos. Além disso, outros traços foliares, que capturam a composição química, estrutura celular e morfologia interna, podem ser medidos com o uso da técnica de Espectroscopia de Infravermelho Próximo (FT-NIR). Esta ferramenta captura a quantidade e qualidade de uma luz que é absorvida pelo tecido de folhas quando irradiados com luz de faixa de comprimento de onda conhecida. Assim, as respostas espectrais assemelham-se às impressões digitais de cada indivíduo e também podem ser usadas para caracterizar a variabilidade entre os indivíduos.

Arumãs (Figura 1) são plantas do gênero *Ischnosiphon*, cultural e economicamente importantes para vários povos indígenas da Amazônia que usam suas fibras na fabricação de cestos e peneiras de mandioca. Estes organismos exibem uma grande variação morfológica ao longo da sua distribuição geográfica. Devido à grande diversidade morfológica dos Arumãs, a delimitação de espécies tem sido problemática. Isso faz com que as espécies de Arumã sejam um grupo ideal para estudar como o fenótipo reflete o caminho evolutivo de onde essa variabilidade surge.

Atualmente, a identificação de espécies de *Ischnosiphon* continua sendo problemática para usuários, tanto taxonomistas quanto ecólogos, devido principalmente à enorme variabilidade morfológica sob os nomes das espécies; a dificuldade de perceber os critérios dessa categorização e as circunscrições propostas para muitas espécies, e também devido ao grande número de informações sobre o hábito e caracteres morfológicos ausentes na maioria dos materiais depositados atualmente disponíveis.

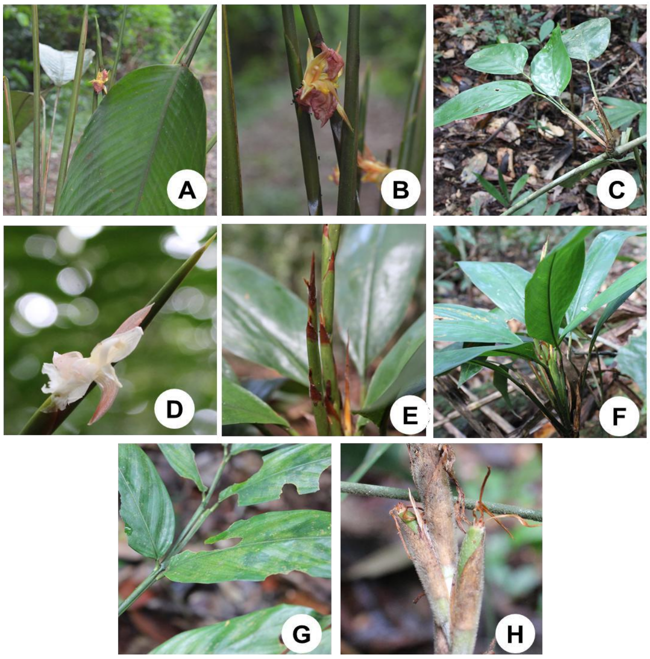

Figura 1. Diferentes espécies de Arumã, gênero *Ischnosiphon* Körn. (A-B) *Ischnosiphon obliquus* (Rudge) Körn. Foto: Thiago André; (C-D) *Ischnosiphon puberulus* Loes .; (E-F) *Ischnosiphon martianus* Eichler ex Petersen; (G-H) *Ischnosiphon crassispicus* L. Andersson. Foto: María A. Buitrago.

Traços morfológicos das plantas estão acessíveis em coleções botânicas, também conhecidas como herbários, em todo o mundo. Essas coleções são semelhantes às bibliotecas, mas, em vez de livros, preservam plantas inteiras ou partes representativas delas que são denominados espécimes.

O primeiro passo após a seleção do material dos herbários foi obter informações morfológicas e espectrais individuais de cada espécie de Arumã. As espécies são representadas na natureza por indivíduos, portanto, espera-se que cada espécime represente formas diferentes ou similares que uma espécie poderia ter. Para isso, um total de 60 variáveis morfológicas foram medidas em 244 espécimes de 22 espécies, utilizando uma plataforma pública para análise de imagens científicas. Da mesma forma, as características espectrais também foram medidas a partir de folhas de amostras dos herbários do INPA e NY. Os tecidos das folhas foram irradiados diretamente com a ajuda de um espectrofotômetro, e as respostas espectrais foram analisadas.

A segunda etapa consistiu em reunir informações sobre as condições em que essas plantas vivem. Dados sobre o clima (temperatura, precipitação, radiação solar, etc.) e coordenadas geográficas foram baixados dos repositórios *online* da biodiversidade.

O terceiro passo foi descrever a variação morfológica e espectral das espécies de Arumã e detectar se houve ou não relação com as variáveis ambientais. Descrever a variação dessas características pode indicar se a classificação atual dos Arumãs contempla variações individuais. De fato, os resultados das análises de variação de características indicaram que as espécies de Arumãs são muito mais complexas de se definir usarmos apenas caracteres morfológicos. Existem indivíduos de várias espécies que se sobrepõe, ou seja, que não se enquadram nas categorias definidas pelos cientistas.

Agora, sabendo como algumas espécies de Arumã variam, existem outros tipos de análise que podem revelar se essa variação na forma, tamanho e respostas espectrais está relacionada ao meio ambiente. Usando diversas ferramentas, revelamos que algumas espécies de Arumãs são influenciadas por fatores climáticos, mais precisamente pela precipitação e pela temperatura. No entanto, a maioria das espécies de Arumã não tem relação com as variáveis analisadas. Ou seja, é provável que outros fatores estejam influenciando a variação nestas plantas.

Uma melhor compreensão dos indivíduos na natureza permite que as espécies, as unidades que usamos em diferentes áreas da ciência, como na ecologia, evolução e sistemática, tenham um sentido biológico. Propomos um método que pode ser replicado para acomodar a variabilidade individual no diagnóstico de espécies, especialmente. Além disso, é muito importante considerar a interação dos indivíduos com o meio ambiente. Em Arumãs, por exemplo, nem o clima nem a distribuição espacial foram preditores universais de variação de forma, tamanho ou respostas espectrais das espécies.

Há muitos processos ecológicos e evolutivos no comando de toda a variação nas formas de vida que apreciamos no mundo.

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Leituras sugeridas

Ahrends A, Rahbek C, Bulling MT et al. 2011. Conservation and the botanist effect. Biological Conservation 144: 131–140.

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Durgante FM, Higuchi N, Almeida A, Vicentini A. 2013. Species Spectral Signature: Discriminating closely related plant species in the Amazon with Near-Infrared Leaf-Spectroscopy. Forest Ecology and Management 209: 240–248.

CHAPTER 1

Phenotypic divergence driven by range attributes and environmental heterogeneity in neotropical understory terrestrial herbs

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Fernando O.G. Figueiredo: Conceptualization and writing review and editing.

Thiago André: Conceptualization, funding acquisition, investigation, methods, resources, writing original draft, review and editing.

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The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Abstract The assessment of morphometric and spectral variation of individuals along species range, including its environmental gradients, can be used to understand drivers of morphological variation, which in turn can underscore delimitation of natural units. We used the rhizomatous herb genus *Ischnosiphon* (Marantaceae) as a model to test this idea due to its great morphological variation and continental distribution. Here, we apply an individual-based approach to test how much morphological and spectral variation in 11 wide to narrowly distributed species of *Ischnosiphon* is explained by environmental factors and geographical distribution. We demonstrate that range size is not a good predictor of phenotypic variance and that climatic distance is often more relevant to morphological and spectral variation than geographic distance. These results provide evidence of how morphological and spectral traits are structured by climate and spatial distribution and how environmental gradients varies in the control of phenotypic variation. Finally, we highlight how interpretation and recognition of species' morphological and spectral limits is prone to underestimation of the role of individual variability and its association to climatic niches.

Keywords: Climate, environmental distance, geographic distance, monocots, Neotropics, phenotype.

Introduction

Plants change along environmental gradients, and consequently, also in the long term of evolutionarily time (Cain 1950). Likewise, morphological divergences studied along ecological and geographic gradients can elucidate if evolutionary processes other than environmental pressures are in charge of species phenotype unrelatedness. Moreover, since different but parallel adaptations to analogous conditions can result in overall form convergence (Box 1996), sampling biological traits from individuals is essential to comprehend biodiversity and the underlying patterns of variation at the level of individuals and populations (Duncan and Baum 1981, Bookstein 1998, Henderson 2006).

Furthermore, spectral patterns of plant tissues can also be used to characterize the variability of individuals. For instance, Near-Infrared Spectroscopy (FT-NIR) is a practical tool that can be used to characterize plant material (Fernandez et al. 2011, Curty 2013, Lang et al. 2015). The spectral response of leaf tissue, when irradiated with incident light of a known wavelength range (Foley et al. 1998), is a function of the chemical composition and structure of cells and internal morphology of the leaf (Ponzoni 2002), which has phylogenetic structure (Durgante et al. 2013) and it is likely characteristic of each individual. These quantitative and qualitative biological traits can be easily measured in dried specimens deposited in biological collections (Stern and Eriksson 1996, Lane 1996).

The genus *Ischnosiphon* is represented by species with wide variable morphological features that make it ideal for investigating the role of environment and geographic distribution on intraspecific variation patterns. These terrestrial rhizomatous herbs inhabit the forest understories along tropical America, being distributed from Nicaragua to south Bolivia and Brazil, displaying diverse range sizes and comprising ca. 36 currently accepted species (Andersson, 1984). These plants are culturally and economically important for several Amazonian indigenous people that use its fibres in the manufacturing of baskets and manioc sifters (Nakazono et al. 2004, Costa et al. 2008).

The exploration of the morphometric and spectral characteristics of *Ischnosiphon* species offers an opportunity to understand how individuals can be modelled by extrinsic factors, and how much of such variation may be species-specific. The purpose of this study is to understand how morphological and spectral traits are structured by environmental heterogeneity and spatial distribution, and how environmental gradients varies in the control of the phenotypic variation of organisms with different range sizes. Finally, we discuss the relevance of phenotypic variability explorations on systematics, evolutionary and ecological studies.

Material and Methods

Herbaria collections from Brazil and the United States were analysed and photographed, particularly specimens deposited in BHCB, INPA, RB and NY herbaria (herbaria acronyms follow Thiers 2019, continuously updated). In addition, available digitized material from other herbaria databases (NY, MO, F, COL, and COAH) and high-resolution images of type collections available in the Global Plant Initiative (GPI) on JSTOR and the FMNH-Botany database were also examined. A total of 11 species were selected based on its taxonomic identification and geographical distribution, prioritizing samples from across species range (Supplementary Data Table S1 and Table S2).

We measured 60 morphological characters (24 vegetative and 36 reproductives, Supplementary Data Table S2) from fixed landmarks that define the locations of particular traits, in a total of 180 individuals, with a mean of 16 specimens per species. Morphometric measurements were performed in the software ImageJ 1.52h (https://imagej.nih.gov/ij/). Since not all morphological characters were available in herbaria material, we eliminated variables with more than 50% of unavailable information. Therefore, each species has a different number of morphometric variables in the analyses considered below.

Spectral variation was gathered from readings of upper and lower leaf surfaces from 114 specimens from INPA and NY herbaria material. Readings were collected for all selected species except for *I. ovatus* from which we had no herbaria material available. A total of two readings per specimen leaf (upper and lower surfaces) were collected with a Thermo Nicollet spectrophotometer, using the Antaris FT-NIR II Method Development System (MDS), available at the Instituto Nacional de Pesquisas da Amazônia-INPA. The average spectrum was calculated from the absorbance values at all wavelengths over the entire FT-NIR spectrum (1000 to 2500 nm) registered from all samples. This set of average wavelengths was analysed to detect the most informative wavelengths selected by stepwise discriminant function (LDA, Fisher 1936, Lang et al. 2015). This function captures the set of independent variables that best predict species identity. To do this we used the step class function of the Klar package (Weihs 2005). A total of 15 wavelengths were selected as the most informative and used in posterior multivariate statistical analyses (Supplementary Data Table S3).

Principal component analyses (PCA) were performed for both the morphological data set containing the characters selected for each species and the spectral data set representing individual absorbance values at the 15 most-informative wavelengths.

Here we defined this dimensionality reduction set by the first three dimensions of the PCA as Morpho-space and Spectral-space, respectively.

To test for climate and geographical control on morphological and spectral traits, we collect coordinate registers of *Ischnosiphon* specimens from herbaria labels and by accessing the Global Biodiversity Information Facility database (GBIF, https://www.gbif.org). Georeferenced localities were checked by comparison to specimen's label information. In addition, we extracted climatic data from the WorldClim 2.0 database (Fick & Hijmans 2017, available at http://www.worldclim.org/) with a spatial resolution of 30 seconds (~1 km^2). A total of 25 climatic variables, 19 standard bioclimatic variables from WorldClim plus maximum, minimum and mean values of Solar radiation and Water vapour pressure, were analysed. Variables are the average for 1970-2000 period.

For each occurrence point of each species' individuals, bioclimatic variables values were extracted using the point sampling tool of QGIS (QGIS Development Team 2017). Since BIOCLIM variables can be correlated, we performed a Spearman's correlation test for the 25 variables to each one of the species analysed. Only a single variable was retained when correlation coefficients were higher than 0.6 or less than -0.6 (Supplementary Data Table S3).

Euclidean distances were calculated to Morpho and Spectral spaces as well as for geographic and bioclimatic datasets. Dissimilarity matrices were obtained using the Vegan package (Oksanen et al. 2016). Since Euclidean dissimilarity matrices need to be standardized we scaled our datasets when running the *vegdist* function.

Partial Mantel Tests (Mantel 1967, Smouse et al. 1986) with 50,000 permutations were performed to correlate morphological and spectral variation with geographic and environmental distances, independently. We calculated the correlation between (1)

Morpho-space and bioclimatic distances, controlling for geographic distance among individuals of each species; (2) Morpho-space and geographic distances, controlling for bioclimatic distance among individual's occurrences of each species; (3) Spectral-space and bioclimatic distances, controlling for geographic distance among individuals of each species and (4) Spectral-space and geographic distances, controlling for bioclimatic distance among individual's occurrences of each species. Statistical analysis were run on R environment (R Development Team 2019).

Further explorations were performed for species that indicated to be morphologically or spectrally correlated with environmental or geographic variables after Mantel tests. Linear regressions were performed to observe the relation between each bioclimatic variable and each of the principal components defining the Morpho and Spectral spaces of each species. Bonferroni corrections were used to evaluate significance of linear regression probabilities.

Occurrence points gathered from GBIF (n=1976) were used to calculate species ranges. Occurrences points were verified manually to detect incongruences in geographic coordinates and identification errors.

We used the heatmap function of QGIS (QGIS Development Team 2017) with 500 kilometres radius distance surrounding occurrence points per species to generate an estimated occurrence layer based on presence evidence in a 1 km^2 raster grid. Grid cells were polygonized and used to calculate the range size of each species. Then, we tested the relationship between range size and the variance of each quantitative morphological and spectral character state using linear models in R.

Results

Principal Component Analyses were able to summarize the morpho-spectral variation among almost all species in the first three dimensions (Supplementary Data Fig.S1 and Fig. S2). The cumulative explanatory power of the three first components of morphometric data combined varies between 48 to 77%. The lowest cumulative proportion of variance explained was observed in *I. leucophaeus* (48%) and *I. obliquus* (49%). Principal components explain more than 70% of the variance in *I. hirsutus, I. longiflorus* and *I. martianus*. In general, species Morpho-space was defined by eight morphological characters. Spathe, sheat and pulvinulus width (X24.1, X7 and X11) determined the Morpho-space of 63% of species. At the same time, Morpho-space of 54% of species was basically defined by lamina length and width (X13 and X12), lamina apex displacement angle (X18), leaf area (X52), radius of a circle with leaf area (X53) and pedicel width (X20.1).

The three main spectral principal components explained > 99% of the total variation of species NIR datasets. Here, Spectral-space was mainly determined by five wavelengths of the spectrum (4319.765, 4724.743, 4778.74, 5149.006 and 5241.572 nm).

The morphological and spectral variation of most studied *Ischnosiphon* species are structured by climatic gradients or geographical distance (Table 1). Partial Mantel tests show that the correlation between morphological variation and climatic distance is significant in *I. gracilis* and *I. ovatus*, after controlling for geographical distance, whereas the correlation between morphological variation and geographical distance is significant in *I. cannoideus*, *I. martianus* and *I. leucophaeus*, after controlling for climatic distance (Table 1). A similar pattern was observed for partial Mantel tests based on species Spectral-space. The correlation between variation in spectral responses and climatic distance is significant in *I. lasiocoleus*, after controlling for geographic distance, whereas the correlation between variation in spectral responses and geographic distance is significant in *I. leucophaeus*, after controlling for climatic distance (Table 1). The only case in which morphometric and spectral variation was significantly correlated with geographic distance after controlling for climatic distance was within *I. leucophaeus*. The correlations between *I.cannoideus* and *I. martianus* Spectral-spaces and geographic distance remained marginally non-significant after controlling for climatic distance ($r= 0.27$, $p <0.070$ and $r= 0.48$, $p <0.083$, respectively). Finally, of the total of species analysed, *I. arouma*, *I. hirsutus*, *I. longiflorus*, *I. obliquus* and *I. puberulus* had no significant correlation with climatic or geographic distances.

Species with morphometric and spectral variation structured by climatic distance showed correlation with variables of precipitation and temperature (Supplementary Data Table S5). The second principal component of *I. gracilis* Morpho-space was positively correlated with precipitation of driest month ($R^2=0.60$, $p<0.005$) (Fig. 1A). Similarly, the second principal component of *I. leucophaeus* Spectral-space was significantly influenced by precipitation of driest month ($R^2=0.36$, $p<0.03$) and by annual mean temperature ($R^2=0.35$, $p<0.03$) (Fig. 1B, C).

Further explorations of range size (Table 2) effects on individual morphological and spectral responses showed that larger ranges do not imply a greater variation in morphological or spectral traits in *Ischnosiphon* species (Supplementary Data Table S6).

Discussion

We analysed *Ischnosiphon* morphometric and spectral spaces relation with climatic and geographic gradients using an individual-based approach, and tested whether range size is associated with species phenotypic variation. We found that climatic distance has a greater influence on morphometric and spectral variations than geographic distance, regardless of species range size. Overall, morphological variation of *Ischnosiphon* species is more difficult to summarize in multidimensional space when compared to spectral variation (Supplementary Data Fig.S1 and Fig. S2). Morphologically dissimilarities within *I. gracilis, I. cannoideus*, *I. leucophaeus, I. martianus* and *I. ovatus* are influenced by climatic factors (Table 1). Nevertheless, climate variation or geographical distance does not always influence morphological and spectral variation within *Ischnosiphon* species. This may indicate that consistent phenotypes have been successfully adapted to a broader range of climatic conditions. Alternatively, other environmental factors not tested here (see Costa 2005, Blach-Overgaard et al. 2010, Figueiredo et al. 2018, Zuquim et al. 2019), such as edaphic conditions, could be driving phenotypic variation. Additionally, variation in environmental factors is difficult to asses at local scales, particularly when intraspecific variation is being investigated.

It is generally expected that spatially closer individuals should be phenotypically more similar since environmental differences can be highly correlated with geographic distance (Dillon 1984). Indeed, we found this to be true in *I. cannoideus* and *I. martianus*. These species are distributed along Central Amazon Basin, with *I. martianus* expanding its range into the Guiana Shield region. Morphological traits varying between individuals of *I. cannoideus* and *I. martianus* are related to the size of the sheath, petiole and lamina (pers. obs.). In addition, *I. cannoideus* have been mostly registered in gallery forests and swamp margins, what could indicate that this species is dependent on water-rich environments or adapted to seasonally flooded ecosystems. On the other hand, registers of *I. martianus* indicate that this species inhabits well-drained grounds of *terra firme* forests. Having access to the local conditions of an individual by accurate geographic records would facilitate the study of the environmental role in biological attributes in nature.

Geographic distribution has no particular effect in the divergence of morphological traits of *I. gracilis* and *I. ovatus* individuals. In both species, climate is the main driver of individual morphological differentiation. Additionally, spectral individual variability within *I. lasiocoleus* is highly structured by climate and not by geographic distribution, which indicates that absorbance responses along near infrared spectra reflect specific local conditions. However, intraspecific spectral variation should be interpreted with caution since leaf phenology highly influences absorbance responses (Chavana-Bryant et al. 2016, Fajardo and Siefert 2016, Wu et al. 2016). Nevertheless, studies yielding leaf spectral traits analyses have been reported to be successful in recognizing (Castillo et al 2008, Krajsek et al. 2008), discriminating (Fan et al. 2010, Durgante et al. 2013, Lang et al. 2015) and delimiting species (Prata et al. 2018). Therefore, further studies should explore habitat effects on individual leaf spectral responses, especially when species diagnosis is the main focus.

The only case in which both morphological and spectral variation was structured by geographical distribution was observed within *I. leucophaeus* individuals (Table 1). One could infer that individuals of this species undergo processes of limitation by distance, what would be expected under a population genetic structured model with lack of environmental constraints to phenotype (van Strien et al. 2015).

When morphological or spectral trait variation is structured by climate we can further explore which variable or group of variables are affecting those individual responses. For instance, we found that the Morpho-space of *I. gracilis* was highly influenced by precipitation of driest month (Fig. 1A).That is, sheath size and lamina symmetry, variables that defined the second principal component of *I. gracilis* morphospace, vary according to the total precipitation that prevails during the driest month. Similarly, the Spectral-space of *I. leucophaeus* is also affected by precipitation of driest month, and the annual mean temperature (Fig. 1B, C). As tropical understory perennial herbs, *Ischnosiphon* performance is thought to be highly related to water availability. In fact, there is evidence of strategies that these plants had developed, such as rhizomes, to survive biotic and abiotic stressors (Chomicki 2013, Munné-Bosch 2014). Local microclimatic conditions related to water availability and temperature can be modelling the shape, size and chemical responses of species (Cavender-Bares and Bazzaz 2000, Asner et al. 2015, Ley et al. 2018, Mori et al. 2019).

All trait variation, environmental and geographic structure analysed here illustrate the importance of considering species as metadata, with data being measured directly from individuals. This allows a better interpretation of species across environmental gradients and encourages a reinterpretation of the categorization of the continuous variability of nature (Hulshof & Swenson 2010). Morphological and spectral trait responses reflect not only the phenotypic complexity of diverse groups of plants, such as *Ischnosiphon*, but also the role of the environment in processes underlying the evolutionary path of all life forms, such as natural selection (e.g. Gabaldón et al. 2013, Wu et al. 2016, Rossoni et al. 2017, Ley et al. 2018). Exploring the relation between intraspecific variation and environmental gradients give us a clear view of the importance of observing in greater detail the continuous variation of characters that are controlled by environmental variables or that respond to the intrinsic properties of lineages. Thus, our results further highlight that traditional categorization of natural organisms and their traits may disregard important phenomena taking place among individuals.

Conclusions

Neither climate nor spatial distribution are universal predictors of trait variability within species. The diversity of causes to phenotypic variation reflect the complex set of ecological and evolutionary processes driving biological diversification. Convergence in phenotype is expected in a scenario of environmental control, which in turn may hamper the recognition and identification of natural entities by arbitrary categorization of species exclusively based on morphology. Hence, our results stress the importance of understanding individual variation for systematics, evolutionary and ecological studies.

SUPPORTING INFORMATION

Supporting information is available at: https://drive.google.com/drive/folders/1PRNAvxUDgSe5RU2dALbLAGTkwzFGmFMe?usp=sharing

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Tables

Species	Morphometrics Partial Mantel Test				FT-NIR Partial Mantel Test			
	Morpho-space vs. Envdist (controlling Geodist)		Morpho-space vs. Geodist (controlling Envdist)		Spectral-space vs. Envdist (controlling Geodist)		Spectral-space vs. Geodist (controlling Envdist)	
	r^2	p	r^2	p	r^2	p	r^2	p
I. arouma	-0.211	0.936	0.041	0.358	0.169	0.132	-0.119	0.762
I. cannoideus	-0.154	0.788	0.460	**0.005**	-0.106	0.715	0.279	*0.070*
I. gracilis	0.289	**0.035**	-0.158	0.859	1	0.667	-1	1
I. hirsutus	-0.129	0.880	0.123	0.127	0.016	0.431	-0.029	0.599
I. lasiocoleus	-0.067	0.622	0.056	0.391	0.372	**0.028**	-0.229	0.861
I. leucophaeus	-0.099	0.889	0.169	**0.016**	-0.087	0.791	0.169	**0.048**
I. longiflorus	0.108	0.296	-0.322	0.940	-0.016	0.517	-0.116	0.681
I. martianus	-0.320	0.899	0.713	**0.009**	-0.163	0.695	0.484	*0.083*
I. obliquus	-0.016	0.503	-0.124	0.759	0.033	0.418	-0.133	0.728
I. ovatus	0.422	**0.046**	-0.009	0.501	—	—	—	—
I. puberulus	0.188	0.129	0.091	0.231	0.014	0.450	-0.024	0.535

Table 1: Partial Mantel tests show the correlation between Morpho and Spectral spaces distance and environmental distance (Envdist) controlling for geographic distance (Geodist), as well as Morpho and Spectral spaces distance and Geodist controlling for Envdist. Significance at $p< 0.05$ is indicated by bold numbers. Marginally non-significant correlations are indicated in italics.

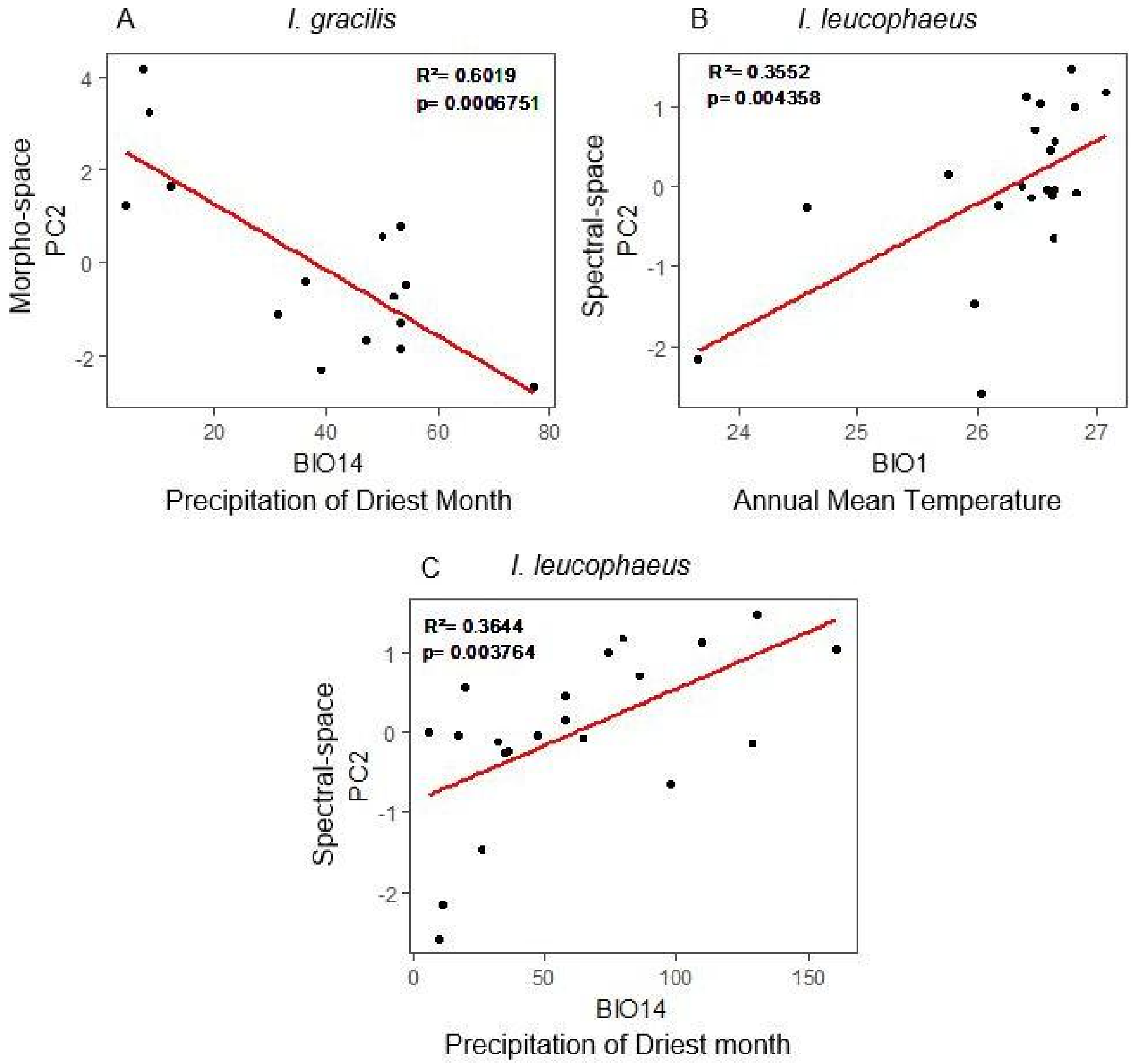
Species	Range size (x10^3 ha)	Distribution
I. arouma	396,650	Panamá, Chocó (Pacific Colombia), northern Venezuela, the Lesser Antilles, the Guianas and Amazon Basin
I. cannoideus	90,285	Central Amazon Basin and upper Rio Orinoco
I. gracilis	301,317	Venezuela, Suriname, French Guiana, Amapá, Amazonas, Pará, Pernambuco and Bahia Brazilian states, and Peru (Loreto)
I. hirsutus	191,459	Amazon Basin
I. lasiocoleus	126,934	Amazon Basin (Rio Branco, Rio Madeira)
I. leucophaeus	425,605	Central America (Nicaragua), Colombia, Venezuela, Suriname, French Guiana, Orinoco drainage, Amazon Basin (Colombia, Brazil, Perú, Bolivia), Pacific coast (Colombia and Ecuador)
I. longiflorus	75,560	Amazon Basin, South Suriname, Amazon Brazilian state (Manaus)
I. martianus	73,129	Suriname, French Guiana, Amapá, Amazonas ,Pará and Rondônia Brazilian states
I. obliquus	308,312	North Colombia, the Orinoco delta, The Guianas, the lesser Antilles and Amazon
I. ovatus	48,910	Brazil Atlantic coast (Rio de Janeiro, Blumenau, Sta Catarina)
I. puberulus	315,592	Central and West Amazon Basin (Brazil, Ecuador, Perú)
Total area	2,353,752	

Table 2 : Range sizes and geographic distribution of *Ischnosiphon* species.

Figure legends

Fig. 1: Morpho and Spectral spaces of *Ischnosiphon gracilis* and *I. leucophaeus* relation to climatic variables. (A) Correlation between BIO14 (Precipitation of Driest Month) and morphometric second principal component within *I. gracilis*. (B, C) Correlations between spectral second principal component and BIO1 (Annual Mean Temperature) and BIO14 (Precipitation of Driest Month) within *I. leucophaeus*.

Figures


A
I. gracilis
R²= 0.6019
p= 0.0006751
Morpho-space PC2
4
2
0
-2
20
40
60
80
BIO14
Precipitation of Driest Month
B
I. leucophaeus
R²= 0.3552
p= 0.004358
Spectral-space PC2
1
0
-1
-2
24
25
26
27
BIO1
Annual Mean Temperature
C
I. leucophaeus
R²= 0.3644
p= 0.003764
Spectral-space PC2
1
0
-1
-2
0
50
100
150
BIO14
Precipitation of Driest month

CHAPTER 2

Accommodating individual variability in species diagnosis on the morphologically diverse *Ischnosiphon* (Marantaceae)

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Original Article

Accommodating individual variability in species diagnosis on the morphologically diverse *Ischnosiphon* (Marantaceae)

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Running title: Individual variability in *Ischnosiphon.*

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Background and Aims: Recognition and delimitation of taxonomic categories of biological organisms are still challenging and full of controversies. Here we unravel the importance of morphometrics as individual-based variables to disentangle the morphological complexity of plant species. Species within *Ischnosiphon* continue to be problematic for users, taxonomists and ecologists alike, due mainly to the huge morphological variability, the unlikeliness to perceive species criteria and circumscription proposed for many taxa, and also due to the many habitat and vegetative macro-morphological characters lacking in most currently available exsiccates.

Methods: Twenty three morphometric variables were sampled from 228 individuals, belonging to 22 species of *Ischnosiphon*. Principal components and discriminant multivariate analyses were used to describe and identify patterns of morphological variation within *Ischnosiphon*.

Key Results: Individual landmark-assessment analysed with multivariate methods captured morphometric intra-specific diversity and complexity within *Ischnosiphon* species, along with the continuous variation of important morphological traits.

Conclusions: By examining the morphology of *Ischnosiphon* species through individual-landmarks assessment, we demonstrated great diversity and morphological complexity in *Ischnosiphon*, and proposed a replicable and analytical framework to accommodate individual variability in species diagnosis on morphologically diverse plant groups.

Key words: Morphometrics, Neotropics, Shape, Size, South America, Zingiberales.

INTRODUCTION

Recognition and delimitation of taxonomic categories of biological organisms are still challenging and full of controversies. Many practices in the field have not changed for centuries (Mishler, 2009), despite the many advances of last decades in biological systematics. In particular, the main criteria used to diagnose life forms continues to be based mainly on macro-morphological abstract characters, which are often categorical, derived either from cognitive analysis of few samples or single type individuals (Scott and Hallam, 2002; Ahrends *et al.*, 2011; Gomes *et al.*, 2013). In particular, taxonomic units, such as the species, are interpretations of phenomenon taking place among individuals and could, therefore, be thought as metadata, while data itself is gathered from organisms (Dupré, 1981; Ghiselin, 1987; Brogaard, 2004; Assis, 2011). Correspondingly, interdisciplinary approaches considering robust evidence taken from organisms and their environment may yield deeper insights on biological traits, which in turn benefits our understanding of diversity and improve our ability to propose predictive and natural classifications (Stuessy, 2009). In particular, many quantitative and qualitative biological variables can be easily measured in dried specimens already in biological collections (Lane, 1996; Stern and Eriksson, 1996), which in turn can be used to analyse phenotypic differentiation (Henderson, 2006; Chalcoff *et al.*, 2008). The quantification of individual morphological variability enables the use of objective and replicable methods that impact species diagnostic's accuracy. Multidisciplinary approaches exploring species boundaries have gained followers in recent years, mainly, with the rise of genomic data (e.g.: Abreu *et al.*, 2018; Gutiérrez-Larruscain *et al.*, 2018; Niu *et al.*, 2018; Prata *et al.*, 2018). However, many other approaches can be used to record and analyse differences between organisms (e.g.: Fan *et al.*, 2010; Fernandez *et al.*, 2011; Durgante *et al.*, 2013). Morphometrics allows the quantification of differences between organisms (Duncan & Baum, 1981; Bookstein, 1998) and underlying patterns of variation at the level of individuals and populations (Henderson, 2006). Morphometric variables measured in individuals can be used to promote solutions to taxonomic challenges such as registering and diagnosing sub-specific variation and species complexes, and delimiting species (Borba *et al.*, 2002, Pinheiro and Barros, 2007; Chalcoff *et al.*, 2008; Pinheiro and Barros, 2009; Laphitz and Semple, 2015). Furthermore, the use of landmarks, i.e. fixed reference points that define the locations of particular traits, that enables capturing size and shape variability, can reveal evolutionary trends of speciation, such as morphological adaptation (e.g.: Rossoni *et al.*, 2017) and niche specialization (e.g.: Funk *et al.*, 2006; Liu *et al.*, 2013; Cornils and Held, 2014).

The genus *Ischnosiphon* (Marantaceae) provide an ideal study group to examine morphological characters, because it has few diagnostic characters despite a great morphological diversity and complexity. This genus is represented by ca. 36 species (Andersson, 1977; 1984). These are terrestrial rhizomatous herbs of forest understories of tropical America, distributed from Nicaragua to south Bolivia and Brazil. Due to a great morphological diversity within Marantaceae, genera delimitation has been troublesome. Nevertheless, phylogenetic analyses of Marantaceae have found *Ischnosiphon* as monophyletic (Andersson and Chase, 2001; Prince and Kress, 2006; Suksathan *et al.*, 2009; Borchsenius *et al.*, 2012), but it may include *Pleiostachya*, and further phylogenetic work should improve taxon and gene sampling to test species monophyletism. In his work, Andersson (1977) took into account numerous morphological and cytological characters, including chromosome counts and anatomical traits to delimit *Ischnosiphon* species. Nevertheless, Andersson's extensive work is, in many aspects, hard to use due to the low accessibility of many characters, particularlyflowers in herbaria material, and the time consuming and relatively expensive techniques of anatomy and cytogenetics. Even so, in this work, Andersson proposed a generic subdivision of six sections, many of which are based on a single character, frequently microscopic, such as in section *Papilloderma*, defined by the presence of papillae in the abaxial epidermis; or in the section *Longiflori*, which was circumscribed by the thickness of the adaxial hypodermis walls.

Besides Andersson's revision, there are few morphological studies on the *Ischnosiphon* species (Suárez and Galeano, 1996; Costa *et al*., 2018), and none of them thoroughly discusses intraspecific differences of quantitative morphological traits and how the complexity of morphological variation is reflected in the different taxonomic entities proposed to date. Nowadays, identification of *Ischnosiphon* species continues to be problematic for taxonomists and ecologists alike, due mainly to the huge morphological variability under accepted species names; the inexplicit species criteria and circumscription proposed for many taxa, and also due to the many habitat and vegetative macro-morphological characters lacking in most currently available herbaria exsiccates.

Here, we describe the diverse morphological variation present in *Ischnosiphon* using quantitative characters and multivariate analysis. We further identify discriminant patterns of variation, by exploring the characters necessary to diagnose species of this genus from herbaria collections, and propose a replicable and analytical framework to accommodate individual variability in species diagnosis on morphologically diverse plant groups.

MATERIAL AND METHODS

Morphometric Analysis

A total of 228 herbaria specimens were studied (Supplementary Data Table S1). Anderson's (1977; 1984) species and sections circumscriptions were adopted to assign species *a priori*. The following species are scarcely represented in herbaria material and are not considered here: *Ischnosiphon bahiensis*, *I. enigmaticus*, *I. fusiformis*, *I. helenae*, *I. grandibracteatus*, *I. inflatus*, *I. rotundifolius* and *I. ursinus*. All *Ischnosiphon* specimens from INPA, BHCB and RB were photographed and available digital images from NY, MO and COAH virtual herbaria collections were downloaded (herbaria acronyms follow Thiers 2019, continuously updated).

Sixty continuous morphological characters were measured (Table 1), 24 of which are vegetative and 36 reproductive (Supplementary Data Figure S1). Given that many of the morphological characters are missing in herbaria specimens, specially those concerning to floral characters, morphometric variables with more than 50% of unavailable data were removed from further analyses. After this quality control step, a total of 23 characters were analysed, 18 vegetative and five reproductive. In addition, the median of the character values for each species was calculated to replace missing information for downstream multivariate analyses (Supplementary Data Table S2).

Traits were measured in digitized herbaria specimens. Image analyses were conducted in ImageJ (downloaded from https://imagej.nih.gov/ij/, ImageJ 1.52h, Java 1.8.0_112). We performed a calibration based on the length scale present within images, prior to measurement. Landmarks were assessed to each of the considered morphological characters. The oldest structures of each specimen were preferentially measured, however, when the specimen only had one leaf or when landmarks were inaccessible in the exsiccates, the better preserved structures were prioritized for measurements.

Supplementary Data Figure S1 presents details of morphological characters. To visualize the main morphometric differences between species and its variation, density plots were created from the original morphometric data set (Supplementary Data Figure S2).

Ordination of morphometric variability

Intraspecific differences of morphometric traits were analysed using the multivariate method of Principal Component Analysis (PCA) based on measurements of 228 specimens and 23 morphometric variables. Before PCA analyses, all characters were scaled to have unit variance. Since PCA analysis mainly describes the global variation of data, Discriminant Analysis of Principal Components (DAPC) were performed using the *adegenet* v 3.5.3 package for the R software (Jombart *et al*., 2010) to calculate membership probabilities. These probabilities can be interpreted as morphometric proximities of individuals to different clusters. All analyses were performed in R environment (v. 3.3.2; R Core Team, 2019).

RESULTS

Shape and size variability

Descriptive statistics analyses show that the values of morphometric characters are greatly overlapped among species confirming the morphological complexity and diversity in shape and size within *Ischnosiphon* species (Supplementary Data Table S3). In general, the most remarkable morphometric characters to identify *Ischnosiphon*, which are also available in almost all exsiccates, are those related with size and shape of leaves. Indeed, of the total morphometric characters successfully measured, 11 are related with lamina features.

All species of *Ischnosiphon* present laminas with some degree of eccentricity, i.e. the deviation of a form from circularity. *Ischnosiphon cannoideus*, *I. hirsutus*, *I. killipii*, *I. lasiocoleus*, *I. longiflorus*, *I. martianus* and *I. petiolatus* present the most eccentric (values varying between 0.94 and 0.98) and the most symmetric laminas (values of apex displacement angles varying from 1.5° to 3.40°). By contrast, less eccentric (between 0.74 and 0.88) and asymmetrical laminas (9.32°, 17.85° and 14.27° respectively) were found in *I. arouma*, *I. crassispicus* and *I. obliquus*. Other species as *I. puberulus, I. polyphyllus, I. gracilis* and *I. surumuensis* present intermediate values of eccentricity and symmetry of laminas, displaying a continuous morphological variation between individuals (Supplementary Data Table S3).

Although most of the species analysed have asymmetric leaves, we observed that the species with more symmetrical leaves are *I. cerotus*, *I. petiolatus* and *I. paryrizinho*, contrary to the strikingly asymmetrical leaves in *I. puberulus*, *I. obliquus* and *I. crassispicus*. Between these two extremes, the rest of the species show a continuous gradient of leaf symmetry (Fig. 1). *I. annulatus* and *I. foliosus* were not plotted for having less than three samples.

In addition to shape and size, individual-landmarks assessment captured the morphometric intra-specific complexity in *Ischnosiphon*, revealing the presence of morphological complexes as the one formed by *I. gracilis* and *I. puberulus*, explored in more detail below.

Multivariate analysis in individual-based morphometrics

Most species show wide morphological gradients in the principal component analysis, including a vast amount of overlap on both principal components, with the only exception of *I. obliquus*, whose individuals stand apart from the remainders (Fig. 2). Individuals of *I. crassispicus* and *I. macarenae* appear to be at both extremes of the ordination plot, however, the sample sizes for these species are low (three specimens). The first two axes of this morphometric PCA accounted for 60.12% of the total observed variation (Fig. 2). The first axis by itself explains half of the total variation, despite not having any correlation higher than 30% with any particular morphometric variable, on the contrary, the set of variables jointly defines this first axis. The second axis, on the other hand, explains 9.9% of the total variation and is mainly defined by lamina apex displacement (X17, r=0.34), lamina apex displacement angle (X18, r=0.48) and lamina apex angle (X18.1, r=0.39), three lamina variables related with shape; and spathe length (X23, r= 0.40), one reproductive character related with size (Table 1).

Additionally, when Andersson's sections were considered in the two-dimensional morpho-space, we detected an inconspicuous pattern: three groups of overlapping specimens.

The first group is formed by the sect. *Bambusastrum* and sect. *Longiflori*, the second by sect. *Hirsuti* and sect. *Papilloderma,* and the last group contains most of the individuals previously assigned to sect. *Ischnosiphon*.

The value of individual-based morphometrics at 'predicting' species

Posterior membership probabilities were calculated with the DAPC, retaining the first 20 PCs, which explains > 95% of the total variance of the morphological data set. Most individuals are discriminated to their original assigned groups with this set of morphometric variables. The overall proportion of individual assignment is 62% when species are provided as the *a priori* groups and 81% when sections are analysed (Supplementary Data Table S4). In addition, a proportion of 9% of individuals are morphologically more likely to be assigned to another species, while 7% of individuals have higher probabilities to be assigned to a different section than the one originally assigned (Supplementary Data Table S4). To visualize how well-defined morphological clusters are and to analyse each specimen‘s morphological affinity, bar-plots with probabilities of assignment to prior set groups were constructed. We detected the same number of prior clusters, corresponding to the 22 species and five sections initially proposed (Fig. 3A, B). However this clusters present morphometric admixture, especially within *I. cannoideus*, *I. gracilis*, *I. longiflorus, I. puberulus* and *I. surumuensis* individuals.

The I. gracilis and I.puberulus case:

We initially detected a relative narrow morphometric variation among *I. gracilis* and *I. puberulus* species (Fig. 2). Further exploration exclusively with individuals of this complex showed that despite the differentiation of *I. gracilis* individuals, there are intermediate phenotypes of *I. puberulus* overlapping with the former. The first two axes of the PCA based only on these two species explained 61.92% (52.42% and 9.5%) of all morphometric variation (Fig. 4A). The first axis again showed no correlation higher than 30% with any particular morphometric variable, while the second axis was defined by four vegetative and two reproductive variables, sheath width (X7), petiole length (X8), petiole width (X9) and lamina secondary venation angle (X15) for the former, and spathe width (X24 and X24.1), for the later.

Furthermore, the visualization of all morphometric variables distribution revealed that in spite of the great overlap, lamina length and width (from the middle and for the widest point), in addition to the radius of the circle with leaf’s area and total leaf area, are variables that can discriminate individuals of both species (Fig. 4B).

DISCUSSION

Intraspecific morphological variability

We have shown here that individual-based morphometrics can be effectively used to interpret inter-specific complex variation. Moreover, the assessment of morphological variability through landmarks allows the capture not only of variation in size, but also the shape of important discriminant features.

Our results confirmed the complex morphology of *Ischnosiphon* species and explicitly presented its continuous nature both within and between species. The fact that the first axis of the statistic ordination is not strongly correlated with any particular variable (Fig. 2), where all characters contributed almost equally in the definition of this component, emphasizes that most of the morphometric variation is not enough to differentiate *Ischnosiphon* species. Instead, we should explore a robust set of explicit and replicable variables to discriminate taxonomic entities.

Several sympatric species with highly similar morphologies, such as *I. puberulus*, *I. polyphyllus, I. gracilis, I. surumuensis, I. killipii* and *I. longiflorus*, can not be clearly differentiated using categorical morphological concepts. On the other hand, our approach presents high rates of positive identification based on morphometric discriminant functions (Fig. 3). Additionally, qualitative characters, like leaf texture and presence of hairs and waxes, allow a clearer morphological delimitation of species with great morphological overlap as *Ischnosiphon hirsutus*, *I. lasiocoleus, I. cannoideus and I. leucophaeus*. Such combination of evidences highlights the importance of a global and integrative analysis of morphology in complex taxonomic groups. The discriminant analysis used here is shown to be an accurate method to infer membership probabilities (Jombart *et al*. 2010; Pometti *et al*., 2014) and it is especially recommended when large datasets are being used (Excoffier and Heckel, 2006).

The morphological continuum of I. gracilis - I. puberulus complex

So far there is no doubt about the hard work involved in the recognition and delimitation of *Ischnosiphon* species. The case of *I. gracilis - I. puberulus* complex illustrates, in an objective and explicit way, how multivariate morphometrics can be conducted when continuous variation of morphological characters tangles the taxonomist labour. These two species are historically hard to differentiate using herbaria specimens due to the tremendous morphological overlap between them. In fact, in his treatment, Andersson considered the organization of the aerial shoot system as the main, if not the only, discontinuous character to separate morphotypes and eventually, to propose the section *Bambusastrum*, which also includes *I. enigmaticus* and *I. killipii*. However, the organization of shoots systems seems to be equally variable and is not always represented or noted in herbaria specimens, resulting in an impractical criteria when working with preserved material. The morphological variation and almost complete overlap in morphology among species within this complex seem to indicate that *I. gracilis* and *I. puberulus* may be two extremes in the continuous morphological variation of individuals that have been recognized as two different species. In fact, these differences are basically given by the size of the leaves (Andersson, 1984), as evidenced by Figure 4B. Since both species are found in sympatry, it is imperative to yield studies assessing molecular variation and life history of the species, along with more evidence to determine the limits of this morphological variation.

We do not propose that morphomerics should be used alone to recognize species, but rather should be used as a tool to delve into continuous morphological characters. A multidisciplinary and integrative approach to biodiversity description and diagnosis is achievable through the explicit consideration of facts measured at the individual level (specimens in the case of herbaria material), particularly from open access integrated repositories. Likewise, species circumscription stability can arise through factual integration of individual-based biological data. We join others (e.g. Gomes *et al.*, 2013) in the recommendation that species delimitation and identification should be treated as separate processes.

We also showed that different morphological species concepts used today in the identification of the species of the genus *Ischnosiphon* are tremendously difficult to apply, as highlighted by the continuous variation on apex symmetry (Fig. 1), and that macro-morphological characters such as the organization of aerial shoots systems and categorical shapes show no apparent discontinuities in dried specimens within *Ischnosiphon*. In this case, the use of other sources of factual evidence is fundamental to diagnose groups. In addition, our results emphasize the importance of pragmatic recognition and subsequent identification of species, through the generation of objective evidences, and explicit and repeatable methods from an individual approach.

Data quality

Current limitations of this approach for ample use in taxonomy and plant diagnosis are mostly related to the lack of a high number of character-rich specimens in botanical collections. Processing of plant material into herbarium sheets has not been consistently considered in the optimization of morphological evidence preservation, which clearly interferes with the quality of taxonomy work. In the *Ischnosiphon* case, this is one of the greatest limitations to explore morphological characters in herbaria specimens to its highest diagnostic potential, since many of vegetative and floral structures were lacking or were not suitable to be comparatively and standardly analysed, influencing the number and nature of variables one could explore.

CONCLUSION

By examining the morphology of *Ischnosiphon* species through individual-landmarks assessment, we demonstrated great diversity and morphological complexity in *Ischnosiphon*, and proposed a replicable analytical framework to accommodate individual variability in species diagnosis on morphologically diverse plant groups.

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SUPPLEMENTARY DATA

Supplementary data are available online at https://drive.google.com/drive/folders/1WGHbdXrlwFFa-vJdkAyHAJ82E4_fRQ0c?usp=sharing and consist of the followings. Figure S1: Characters assessed to morphometric analysis with respective landmark positions. Figure S2: Density plots of all morphometric variables. Table S1: Specimens selected for morphometric analyses with respective collection code and voucher. Table S2: Morphometric matrix with proportion of unavailable data and final selected specimens. Table S3: Summary of descriptive statics of morphological characters of species in analyses. Table S4: Individual membership probabilities obtained from DAPC analyses.

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Fig. 1. Density plot of lamina symmetry along 21 species of *Ischnosiphon*. From left to right: silhouettes representing leaf apexes from *I. cerotus* (Schunke-Vigo 3216), *I. cannoideus* (Prance 14254), *I. ovatus* (Kuhlmann s.n), *I. puberulus* (Andersson 1776), *I. obliquus* (Plowman 2584) and *I. crassispicus* (Plowman 2584).

Fig. 2 Principal component analysis (PCA) plot of the first two principal component axes for all individuals of *Ischnosiphon* based on morphometric variation. Shaped points refer to sections, coloured shapes refer to species, and vectors to size and shape variables (arrows in orange: abbreviations are provided in Table 1).

Fig. 3. Membership probability obtained from DAPC analyses for each of the 228 individuals of *Ischnosiphon*. (A) Species posterior membership probabilities. (B) Section posterior membership probabilities. Each vertical coloured line represents an individual. Mixtured clusters refers to incongruity between membership posterior assignments. See Figure 2 to species colours.

Fig. 4. Comparative morphology in the *I. gracilis*-*I. puberulus* complex. (A) Principal component analysis (PCA) plot of the first two principal component axes. Coloured points refer to species, and vectors to size and shape variables. (B) Histograms for each morphometric variable. Coloured bins refer to species. See Table 1 for characters code.

Morphometrical characters	Code	PC1	PC2	PC3
Sheath length (cm)	X6	-0.23384863	-0.160634492	-0.12035864
Sheath width (at base) (cm)	X7	-0.05315118	-0.063761063	0.02763753
Sheath width (at widest) (cm)	X7.1	-0.261139	0.028383049	-0.06305704
Petiole length (cm)	X8	-0.14800484	-0.209063311	-0.458522
Petiole width (cm)	X9	-0.23304637	-0.186454622	-0.08030551
Pulvinulus length (cm)	X10	-0.24947929	-0.204268553	-0.01302491
Pulvinulus width (cm)	X11	-0.23705769	-0.023930542	-0.01425053
Lamina length (cm)	X12	-0.23265472	-0.251385271	0.22179608
Lamina width (at middle) (cm)	X13	-0.27653906	-0.102919378	0.0464613
Lamina width (at widest) (cm)	X14	-0.27462996	-0.079253128	0.05092878
Lamina secondary venation angle (°)	X15	-0.10506642	0.141034743	-0.52397679
Lamina secondary venation distance (at widest) (cm)	X16	-0.03991078	0.007595314	-0.17795197
Lamina apex displacement (from the centre) (cm)	X17	-0.22225181	0.342080965	-0.05093128
Lamina apex displacement angle (°)	X18	-0.15010169	0.467773089	-0.11887257
Lamina apex angle (°)	X18.1	-0.13975827	0.389162934	-0.1190337
Peduncle width (cm)	X20	-0.26465545	0.01744733	-0.01154425
Pedicel width (cm)	X20.1	-0.23800594	0.066292956	0.12830174
Spathe length (cm)	X23	-0.10743889	0.400733171	0.25997302
Spathe width (at base) (cm)	X24	-0.1188113	0.176392747	0.28367902
Spathe width (at widest) (cm)	X24.1	-0.21224256	0.179923243	0.12858165
Eccentricity	X51	0.17729938	-0.013304679	0.32969306
Leaf area (cm^2)	X52	-0.26523486	-0.127100387	0.20342857
Leaf radius circle (cm)	X53	-0.26523486	-0.127100387	0.20342857

Table 1. Morphological characters used in morphometric analyses of *Ischnosiphon*. PC1, PC2 and PC3: correlation between the original variables and the first, second and third principal components, respectively.

Fig.1.

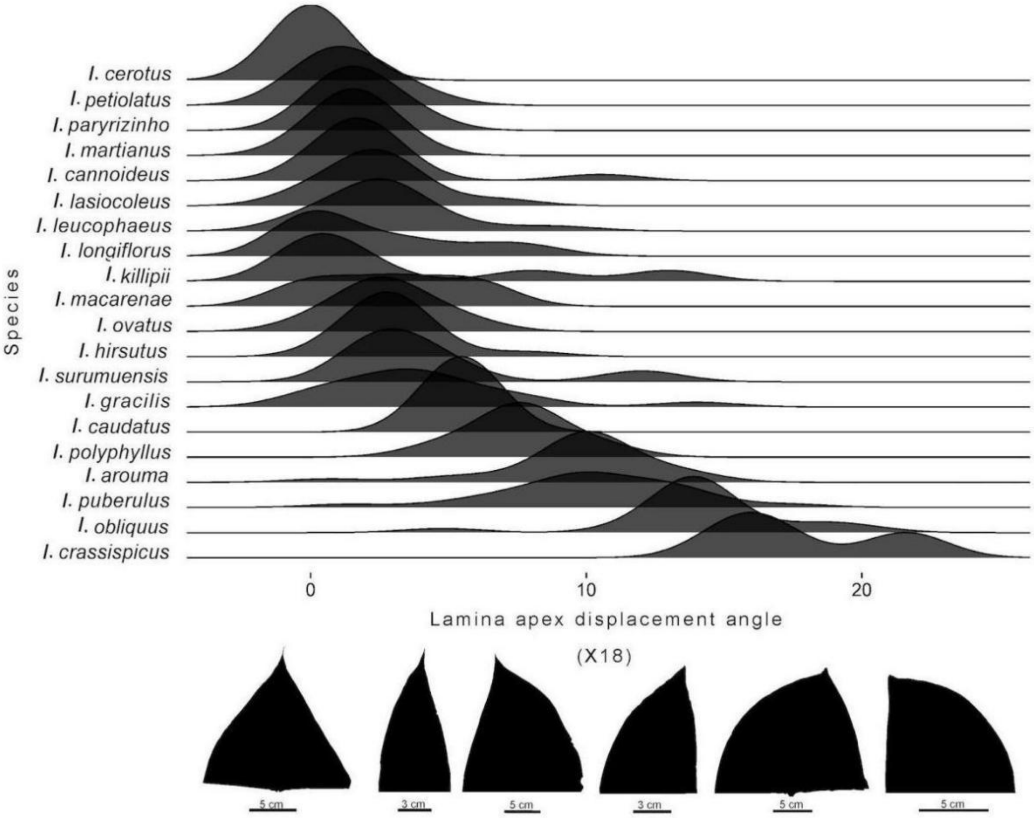

I. cerotus
I. petiolatus
I. paryrizinho
I. martianus
I. cannoideus
I. lasiocoleus
I. leucophaeus
I. longiflorus
I. killipii
I. macarenae
I. ovatus
I. hirsutus
I. surumuensis
I. gracilis
I. caudatus
I. polyphyllus
I. arouma
I. puberulus
I. obliquus
I. crassispicus
Species
0
10
20
Lamina apex displacement angle
(X18)
5 cm
3 cm
5 cm
3 cm
5 cm
5 cm

Fig. 2.

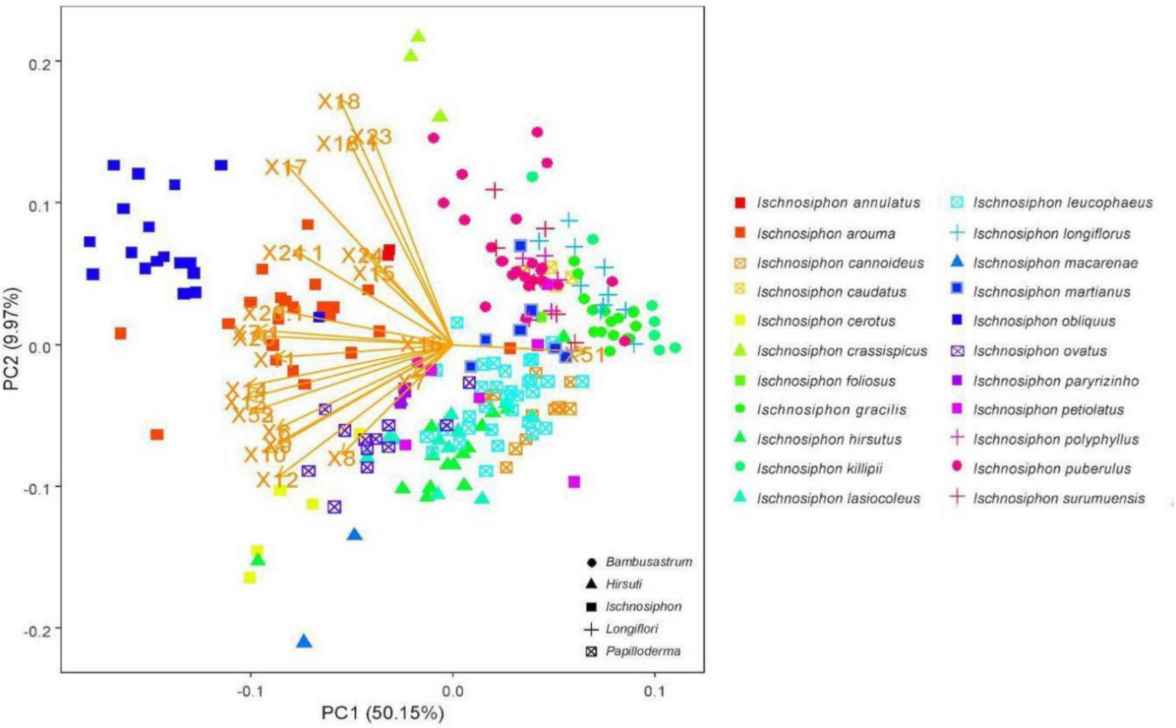

0.2
0.1
0.0
-0.1
-0.2
PC2 (9.97%)
-0.1
0.0
0.1
PC1 (50.15%)
X18
X18.1
X23
X17
X24.1
X24
X15
X20.1
X21
X20
X11
X14
X13
X53
X6
X9
X10
X8
X12
X19
X7
X51
Bambusastrum
Hirsuti
Ischnosiphon
Longiflori
Papilloderma
Ischnosiphon annulatus
Ischnosiphon arouma
Ischnosiphon cannoideus
Ischnosiphon caudatus
Ischnosiphon cerotus
Ischnosiphon crassispicus
Ischnosiphon foliosus
Ischnosiphon gracilis
Ischnosiphon hirsutus
Ischnosiphon killipii
Ischnosiphon lasiocoleus
Ischnosiphon leucophaeus
Ischnosiphon longiflorus
Ischnosiphon macarenae
Ischnosiphon martianus
Ischnosiphon obliquus
Ischnosiphon ovatus
Ischnosiphon paryrizinho
Ischnosiphon petiolatus
Ischnosiphon polyphyllus
Ischnosiphon puberulus
Ischnosiphon surumuensis

Fig. 3.

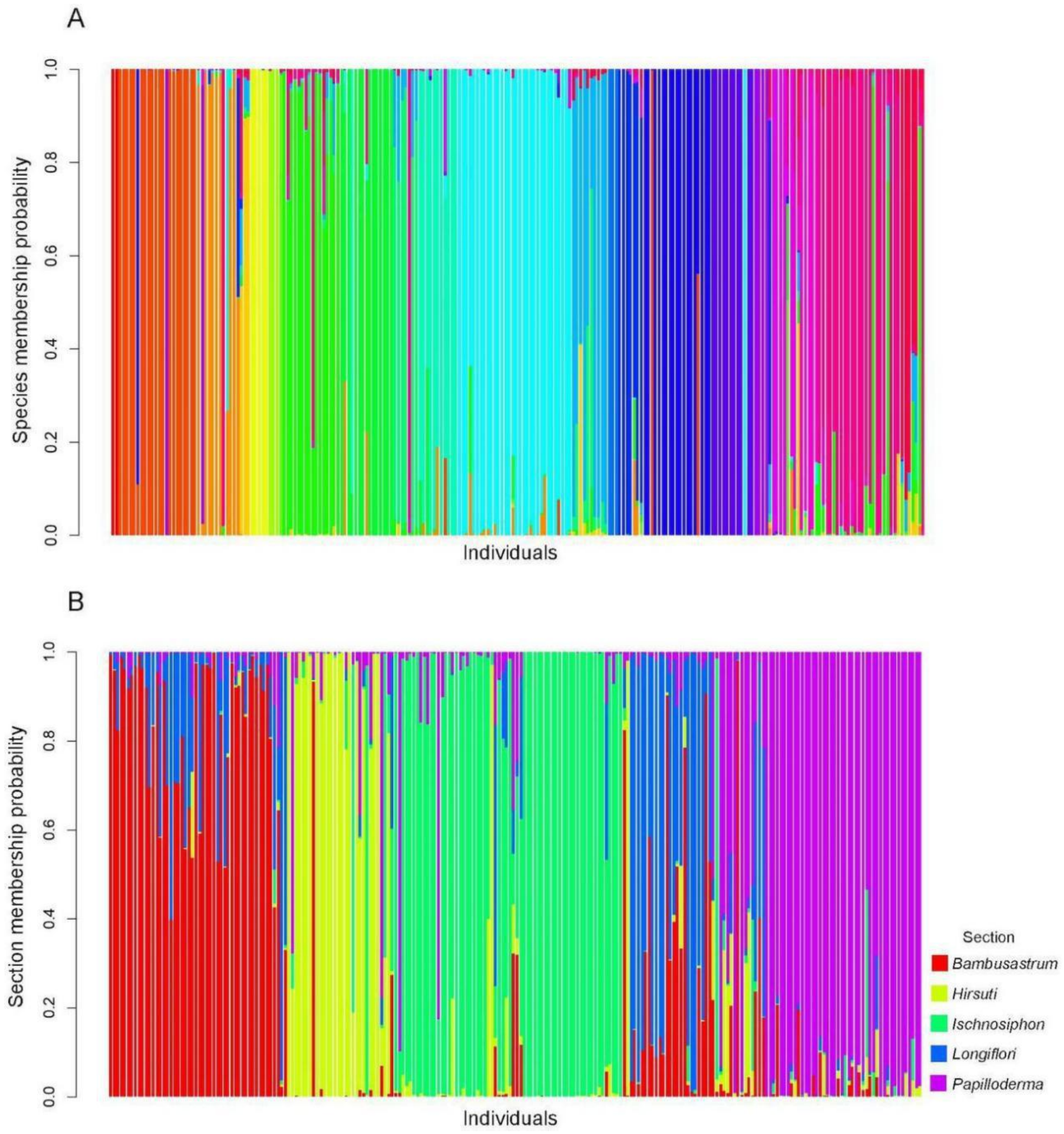
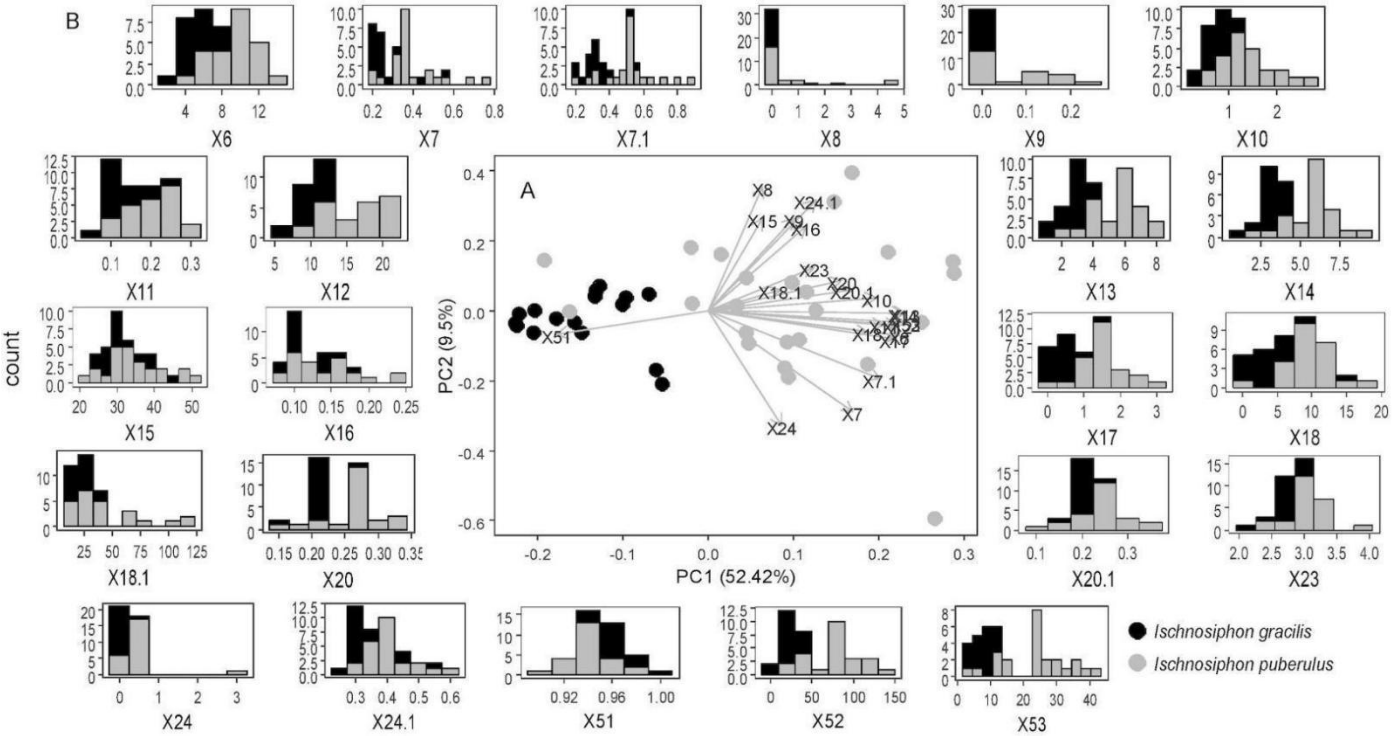

A
Species membership probability
0.0
0.2
0.4
0.6
0.8
1.0
Individuals
B
Section membership probability
0.0
0.2
0.4
0.6
0.8
1.0
Individuals
Section
Bambusastrum
Hirsuti
Ischnosiphon
Longiflori
Papilloderma

Fig. 4.


B
count
X6
X7
X7.1
X8
X9
X10
X11
X12
X13
X14
X15
X16
X17
X18
X18.1
X20
X20.1
X23
X24
X24.1
X51
X52
X53
A
PC1 (52.42%)
PC2 (9.5%)
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.2
0.0
-0.2
-0.4
-0.6
X8
X24.1
X15
X9
X16
X23
X18.1
X20
X20.1
X10
X14
X13
X52
X18
X6
X17
X7.1
X7
X24
X51
● Ischnosiphon gracilis
● Ischnosiphon puberulus

FINAL REMARKS

Individual-based approaches exploring trait variation between different groups of organisms is vital to promote solutions to taxonomic challenges such as delimiting species complexes and defining species boundaries, as well as understanding origins of biological diversity. As presented here, the genus *Ischnosiphon* displays great morphological overlap translated in large varieties of shapes and sizes, indicating that much more effort must be dedicated in the exploration of new evidence that reflects the evolutionary path of these plants.

Furthermore, multidisciplinary and integrative methods applied to biodiversity description and diagnosis are achievable through the explicit consideration of facts easily gathered from already available material, particularly from biological collections and open access integrated repositories. Non-destructive and cost-effective tools such as spectroscopy and morphometrics are powerful to disentangle complex groups.

Likewise, some *Ischnosiphon* species such as *I. gracilis* and *I. leucophaeus* are highly influenced by precipitation and temperature variables. Thus, exploring the relation between environmental gradients and species variability is important to understand the phenomena taking place among individuals.

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Identificação da Dissertação

Título	**GEOGRAPHICAL STRUCTURE OF MORPHOLOGY AND SPECTRAL DIVERSITY IN ARUMÃS (*ISCHNOSIPHON* KÖRN., MARANTACEAE)**

Informações ao revisor

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- **O prazo para avaliação é de 30 dias a partir do recebimento da dissertação em formato digital.**
- **Comentários, correções e sugestões podem ser feitas diretamente no arquivo do projeto ou em arquivo separado, a sua preferência. No caso dos arquivos PDF, podem ser adicionados comentários em trechos selecionados, por exemplo. O arquivo da dissertação comentada será enviado ao candidato e ao orientador. Este parecer não é enviado ao candidato e orientador.**

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Parágrafo Único – O orientador e o discente encaminharão documento assinado sugerindo 5 (cinco) nomes de possíveis avaliadores pré-contactados, com seus respectivos endereço eletrônico e telefone.

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DA APROVAÇÃO OU REPROVAÇÃO DA DISSERTAÇÃO

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I - Aprovado: indica que o revisor aprova a dissertaçãos em correções ou com correções mínimas;

II - Aprovado com Correções: indica que o avaliador aprova o projeto com correções extensas,mas que a dissertação não precisa retornar ao avaliador para reavaliação;

III - Necessita Revisão: indica que há necessidade de reformulação do trabalho e que o avaliadorquer reavaliar a nova versão da dissertação antes de emitir uma decisão final;

IV - Reprovado: indica que a dissertaçãonão é adequada, nem com modificações substanciais.

§ 1o - O Programa preservará o anonimato dos avaliadores da dissertação, exceto se o avaliadoroptar por se identificar na ficha de avaliação encaminhada ao discente e seu orientador.

Art. 63 – O Acadêmico será considerado aprovado caso ao menos dois membros avaliadores emitirem parecer pareceres A ou AC.

Art. 64 – Em caso de reprovação poderá ser concedida, por recomendação dos avaliadores, uma segunda oportunidade ao candidato que, num período máximo de 30 (trinta) dias, a contar da data da avaliação, deverá submeter ao Colegiado a nova versão da dissertação para avaliação.

Parágrafo único – Em caso da não entrega da nova versão da dissertação à Secretaria do Programa no prazo estabelecido ou em caso de reprovação nesta segunda chance, o estudante será automaticamente desligado do curso.

Art. 65 - O Acadêmico que teve sua dissertação aprovada deverá apresenta-la em sessão pública com duração de 40-50 minutos, no prazo máximo de vínculo com o curso, ou seja, 24 meses desde o ingresso."

Comentários à coordenação do PPGBEES:

A dissertação indica que a aluna atingiu o nível esperado para um aluno de mestrado, tendo sido capaz de formular claramente suas perguntas, hipóteses, testá-las e apresentar seus resultados. Portanto, considero que está apta a defender a dissertação e receber o título de mestre.

Tenho uma série de sugestões e críticas específicas, que estão marcadas ao longo de todo o texto. È claro que o texto precisa de uma revisão do inglês para publicação. Como comentário geral, sugiro que a aluna procure ser mais específica em suas afirmações, que muitas vezes são vagas ou abstratas demais.

O capitulo 2 está quase pronto para ser submetido para publicação, e fiz várias considerações que podem ajudar a atingir esta meta.

O capítulo 1 é o que está menos desenvolvido, e sobre o qual tenho sérias dúvidas sobre a interpretação dos resultados e suas conclusões, que a meu ver, não são suportadas pelas análises apresentadas. Este precisa ser revisto.

O titulo da dissertação e as paginas iniciais não deveriam ser em português¿ Até onde sei, isso é o que a CAPES exige.

Avaliação final do projeto de dissertação de mestrado

I - Aprovado (x)

indica que o revisor aprova a dissertação sem correções ou com correções mínimas

II - Aprovado com Correções (x)

indica que o avaliador aprova o projeto com correçõe extensas,mas que a dissertação não precisa retornar ao avaliador para reavaliação

III - Necessita Revisão ( )

indica que há necessidade de reformulação do trabalho e que avaliadorquer reavaliar a nova versão da dissertação antes de emitir uma decisão final

IV - Reprovado ( )

indica que a dissertação não é adequada, nem com modificações substanciais

Identificação do membro da banca:

Deseja identificar-se ao candidato e orientador(es): (x) Sim ( ) Não

Data:24/07/2019

Assinatura:

FORMULÁRIO DE AVALIAÇÃO DE DISSERTAÇÃO DE MESTRADO

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§ 2º – O aluno deverá entregar ao Colegiado junto ao requerimento de avaliação, um arquivo digital da dissertação, para que seja encaminhada aos membros da Banca Examinadora.

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II - Aprovado com Correções: indica que o avaliador aprova o projeto com correções extensas, mas que a dissertação não precisa retornar ao avaliador para reavaliação;

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IV - Reprovado: indica que a dissertação não é adequada, nem com modificações substanciais.

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Art. 64 – Em caso de reprovação poderá ser concedida, por recomendação dos avaliadores, uma segunda oportunidade ao candidato que, num período máximo de 30 (trinta) dias, a contar da data da avaliação, deverá submeter ao Colegiado a nova versão da dissertação para avaliação.

Parágrafo único – Em caso da não entrega da nova versão da dissertação à Secretaria do Programa no prazo estabelecido ou em caso de reprovação nesta segunda chance, o estudante será automaticamente desligado do curso.

Art. 65 - O Acadêmico que teve sua dissertação aprovada deverá apresenta-la em sessão pública com duração de 40-50 minutos, no prazo máximo de vínculo com o curso, ou seja, 24 meses desde o ingresso."

Comentários à coordenação do PPGBEES:

A dissertação apresentada conta com 2 capítulos interessantes e bem estruturados. O tema abordado é importante e atual. Consequentemente, cada capítulo tem grande potencial para publicação em periódicos internacionais.

Apesar de achar o capítulo 1 mais inovador, achei que os resultados do segundo capítulo foram melhor explorados. Essa foi a única razão para "aprovar com correções". Por favor, vejam os comentários ao longo do PDF.

Gostaria de parabenizar a aluna e orientadores pelo excelente trabalho. Não é todo dia que deparo com dissertações de mestrado com dois capítulos, ainda mais com grande potencial como apresentado aqui. Parabéns!

Avaliação final do projeto de dissertação de mestrado

I - Aprovado (   )

indica que o revisor aprova a dissertaçãos em correções ou com correções mínimas

II - Aprovado com Correções (X)

indica que o avaliador aprova o projeto com correçõe extensas,mas que a dissertação não precisa retornar ao avaliador para reavaliação

III - Necessita Revisão (   )

indica que há necessidade de reformulação do trabalho e que avaliadorquer reavaliar a nova versão da dissertação antes de emitir uma decisão final

IV - Reprovado (   )

indica que a dissertação não é adequada, nem com modificações substanciais

Identificação do membro da banca:

Deseja identificar-se ao candidato e orientador(es): (X) Sim (   ) Não

Data: 15/07/2019

Assinatura:

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§ 1o - O Programa preservará o anonimato dos avaliadores da dissertação, exceto se o avaliadoroptar por se identificar na ficha de avaliação encaminhada ao discente e seu orientador.

Art. 63 – O Acadêmico será considerado aprovado caso ao menos dois membros avaliadores emitirem parecer pareceres A ou AC.

Art. 64 – Em caso de reprovação poderá ser concedida, por recomendação dos avaliadores, uma segunda oportunidade ao candidato que, num período máximo de 30 (trinta) dias, a contar da data da avaliação, deverá submeter ao Colegiado a nova versão da dissertação para avaliação.

Parágrafo único – Em caso da não entrega da nova versão da dissertação à Secretaria do Programa no prazo estabelecido ou em caso de reprovação nesta segunda chance, o estudante será automaticamente desligado do curso.

Art. 65 - O Acadêmico que teve sua dissertação aprovada deverá apresenta-la em sessão pública com duração de 40-50 minutos, no prazo máximo de vínculo com o curso, ou seja, 24 meses desde o ingresso."

Comentários à coordenação do PPGBEES:

Prezados,

A dissertação apresenta dois capítulos de elevada qualidade, com excelente potencial de publicação. Foram feitas algumas sugestões e correções, e questionamentos pontuais na metodologia do primeiro capítulo e nos resultados do segundo capítulo. Considero o trabalho aprovado com mínimas correções. Parabéns à discente pelo excelente trabalho, e também aos orientadores.

Avaliação final do projeto de dissertação de mestrado

I - Aprovado (X)

indica que o revisor aprova a dissertaçãos em correções ou com correções mínimas

II - Aprovado com Correções (   )

indica que o avaliador aprova o projeto com correçõe extensas,mas que a dissertação não precisa retornar ao avaliador para reavaliação

III - Necessita Revisão (   )

indica que há necessidade de reformulação do trabalho e que avaliadorquer reavaliar a nova versão da dissertação antes de emitir uma decisão final

IV - Reprovado (   )

indica que a dissertação não é adequada, nem com modificações substanciais

Identificação do membro da banca: Thaís Elias Almeida

Deseja identificar-se ao candidato e orientador(es): (X) Sim (   ) Não

Data: 15/07/2019

Assinatura:

Thaís Elias Almeida

Dr.ª Thaís Elias Almeida
Profª Adjunta - Siape 2143049