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Research Article

Phylogeny, evolution and ecological speciation analyses of *Imperata* (Poaceae: Andropogoneae) in the Neotropics

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Imperata is a ubiquitous grass genus of the tribe Andropogoneae (Poaceae), distributed throughout the world. Previous systematic studies had established that the genus encompasses nine species although no phylogenetic molecular studies are available in which all the taxa have been included. The American continent has the largest number of species, encouraging research into how these taxa have evolved. Here we present a phylogenetic analysis based on three plastids (*ndhF*, *trnL-F,* and *atpB-rbcL*) and one nuclear (ITS) marker that cover the most extensive geographic distribution of the genus. We use this phylogeny to test the monophyly of *Imperata* within tribe Andropogoneae, analyze the infrageneric relationships of the genus, and estimate lineage divergence time. Additionally, ecological niche models (ENM) of the American lineages are presented to recognize the abiotic factors that constraint their potential geographic distribution and allow an understanding of the ecological drivers for species diversification. Our results yield a fully supported tree where monophyly is confirmed for the genus and exposes the existence of two clades, one encompassing five American lineages and the other encompassing those of the rest of the world. In parallel, molecular dating, ENM, and ecological speciation tests suggest that American lineages underwent speciation during the Quaternary associated with conservatism and niche divergence. Our results contribute to both the taxonomic and to the evolutionary knowledge of grasses, and also to the understanding of the biological diversity in the Neotropics.

Key words: ecological niche model, *Imperata*, molecular dating, niche conservatism, niche divergence, plant systematics

Introduction

Recognizing the limits of species and the ecological factors that promote speciation is crucial in the study and understanding of biodiversity (Coyne et al., 2004; Givnish, 2010; Leavitt et al., 2015; Mayden, 1999). The approach to species delimitation and the speciation process using a combination of phylogenetic analysis and ecological niche modelling (ENM) has proven highly effective in solving taxonomic and evolutionary issues in plants.(Alvarado-Sizzo et al., 2018; Duan et al., 2019; Nakazato et al., 2010; Ruiz-Sanchez & Sosa, 2010; Shao et al., 2020; Su et al., 2015). Phylogenetic analysis with molecular data enables inferring relationships and find lineages that can be treated as phylogenetic species (Cavalli-Sforza & Edwards, 1967; Felsenstein, 1981; Hennig, 1966). The speciation process can be studied from an ecological perspective by ENM since species occur in different ecological settings, and adaptation to them leads to evolutionary divergence (Wiens, 2004). In addition, ecological factors can promote speciation by reproductive isolation, thus causing populations to separate through adaptations either to different environments by niche divergence or by retaining ancestral ecological characteristics through niche conservation processes (Graham et al., 2004; Schluter, 2001; Wiens, 2004; Wiens & Graham, 2005).

The Neotropical region extending from Central Mexico to Argentina harbours a high species richness and includes several biodiversity hotspots (C. E. Hughes et al., 2013; Morrone, 2014). There are different hypotheses to explain the origin of the Neotropical diversity, although it is necessary to fill certain gaps in the knowledge and understanding the origins, evolution, maintenance, and patterns of distribution of biodiversity (Antonelli et al., 2018). According to (Giudicelli et al., 2019) most of the plant diversification studies in South

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America have been focused on tropical forests and species of Andean origin, while there are fewer studies on grassland ecosystems. The grassland ecosystems in the Neotropics are mainly inhabited by C4 grasses, including members of the tribe Andropogoneae Dumort (Poaceae), which occupy large areas (Cabido et al., 1997; Kirschner & Hoorn, 2020). The expansion of C4 grasses in the Americas occurred during the late Miocene-Pliocene (Edwards et al., 2010; Strömberg, 2011). Therefore, representatives of Andropogoneae constitute models of great value for the understanding of the evolution of grasses in the Neotropics.

The genus *Imperata* Cirillo is a rhizomatous perennial grass with C4 photosynthesis inhabiting the tropics and warm temperate regions of the world (Gabel, 1982). This genus is characterized mainly by inflorescences contracted, superficially spike-like, and covered with long silvery hairs (Kellogg & Kubitzki, 2015). Taxonomically, *Imperata* –by means of morphological and molecular evidence– has been included in the tribe Andropogoneae, subtribe Saccharinae Griseb (Clayton, 1972; Clayton & Renvoize, 1986; Kellogg & Kubitzki, 2015; Soreng et al., 2017). Later on, Welker et al. (2020) based on phylogenetic evidence of chloroplast and nuclear molecular data (Lloyd Evans et al., 2019; Teerawatananon et al., 2011; Welker et al., 2016, 2020) transferred *Imperata* to the subtribe Germainiinae Clayton. The first comprehensive taxonomic studies for the genus as a whole were made by Hackel (1889) and Gabel (1982). Hackel (1889) carried out a preliminary morphological study and recognized six species and six varieties, while later on Gabel (1982), through phenetic, anatomical, cytological and enzymatic analyses, proposed that the genus congregates nine species. According to Gabel (1982), the main differential traits are anther number (1-2), inflorescence shape, ligule length, and spikelet length. However, there is frequent overlap of morphological traits between species (Gabel, 1982). It is interesting to note that up to now, most molecular phylogenetic studies have included only *Imperata cylindrica* (L.) Raeusch as representative of the genus (Burke et al., 2016; Estep et al., 2014; Hodkinson et al., 2002; Lloyd Evans et al., 2019; Skendzic et al., 2007; Teerawatananon et al., 2011; Welker et al., 2015, 2020), except for Welker et al. (2016), who also included *I. cylindrica*, *I. brasiliensis* Trin. and *I. tenuis* Hack. Thus, a phylogenetic analysis including samples of all the taxa was considered necessary in order to test not only the monophyly of the genus within the Andropogoneae but also to evaluate phylogenetic relationships and infrageneric limits using as a starting point the phenetic study of Gabel (1982). *Imperata* is also interesting for their worldwide distribution (Gabel, 1982): *Imperata cylindrica* is cosmopolitan, but *I. contracta* (Humb., Bonpl. & Kunth) Hitchc., *I. minutiflora* Hack., *I. brasiliensis*, *I. tenuis*, and *I. condensata* Steud. are considered native to South America, although *I. brasiliensis* and *I. contracta* have been introduced in Central and North America. *Imperata brevifolia* Vasey is considered native to North America. *Imperata conferta* (J. Presl) Ohwi and *I. cheesemanii* Hack. are found in Australia and Oceania, the latter being endemism of the Kermadec Islands in New Zealand.

The present study was conducted to integrate phylogenetic and molecular dating, to delimit lineages, and to date cladogenesis events in *Imperata*. Moreover, to inquire about the mechanisms of ecological speciation of *Imperata* in the Neotropics through ecological analyses. First, we tested the monophyly within the tribe Andropogoneae and infrageneric relationships of *Imperata*, based on nuclear and plastid DNA sequence data. Secondly, the phylogeny of *Imperata* was dated to estimate lineages divergence times in order to relate it to past climatic and geological events. Lastly, we constructed ecological niche models (ENM) and tested niche overlap of the American lineages to estimate the importance of abiotic factors in the geographic distribution of the genus in the Americas and to test whether the ecological factors have had an impact on the speciation of the genus in the continent through either niche divergence or niche conservatism.

Materials and methods

Taxon sampling, DNA extraction and amplification

We sampled nineteen specimens of *Imperata* belonging to nine taxa according to the species circumscription proposed by Gabel (1982). The plant material was collected in Argentina and Brazil; in addition, collections from CHR, MA, NYBG, LPB, and SI [abbreviations for herbaria follow 'Index Herbariorum' http://sweetgum.nybg.rg/ih/] were analyzed (see Appendix, Table S1, online supplemental material, which is available from the article's Tylor & Francis Online page at XXX). Q1 Twenty-five specimens were included as outgroup representing 19 genera within the tribe Andropogoneae according to the taxonomic classification proposed by Welker et al. (2020) and a specimen of the genus *Arundinella* Raddi which is the sister group of the tribe Andropogoneae (Estep et al., 2014; Grass Phylogeny Working Group II, 2012; Mathews et al., 2002; Teerawatananon et al., 2011). Four molecular markers were used in this study: three plastid ones (*ndhF, trnL-F,* and *atpB-rbcL*) and a nuclear one (ITS). Total

genomic DNA was extracted from silica-dried leaves of both the *Imperata* samples collected in the field and the herbarium samples using the CTAB method (Khanuja et al., 1999). From the extracted DNA, plastid markers and ITS were amplified using polymerase chain reaction (PCR). PCR conditions and primers that were used to amplify the plastid and ITS regions are listed in Table S2 (see supplemental material online). The amplification products were separated by electrophoresis in 1% agarose gel TBE and visualized under UV light after staining with SYBR Safe gel stain (Invitrogen, Carlsbad, California, USA). The amplified products were sent to Macrogen Inc. (Seoul, South Korea) for purification and sequencing. For this study, we obtained new sequences for eighteen out of nineteen *Imperata* specimens, and the sequences of an *Imperata* specimen and specimens used as outgroup were downloaded from GenBank (http://www.ncbi.nlm.nih.gov). Some of the *Imperata* taxa and those used as outgroup are not represented by all markers. Voucher specimens and GenBank accession numbers of the plastid markers and ITS sequences of *Imperata* and specimens used as outgroup are listed in Tables S3 and S4, respectively (see supplemental material online).

Sequences and phylogenetic analyses

Sequence chromatograms obtained from sequencing were checked for quality and a consensus sequence was obtained comparing forward and reverse sequences using the Clustal W algorithm (Thompson et al., 1994) as implemented in BIOEDIT v7.1.3 (Hall, 1999). When ambiguities appeared between both sequences, the corresponding letter is placed according to the IUPA nucleotide code. All sequences were aligned using MAFFT v7 (Katoh et al., 2019), followed by the manual removal of ambiguous alignments using ALIVIEW v1.26 (Larsson, 2014). Missing sequences were treated as missing data. To evaluate congruence between the plastid and ITS data, datasets were tested with the incongruence length difference test (ILD) (Farris et al., 1995) implemented in PAUP v4.0a167 (Swofford, 2002) as the partition homogeneity test. As suggested by Pelser et al. (2010), to reduce the chance of false positive, only a partition homogeneity test *p*-value below 0.01 was considered as evidence of significant incongruence. To test the monophyly of *Imperata* within tribe Andropogoneae and to resolve the infrageneric relationships, we carried out phylogenetic analyses using Maximum Likelihood (ML) and Bayesian Inference (BI; Mau et al., 1999; Rannala & Yang, 1996). Five matrices were analyzed: the ITS matrix, a matrix combining all plastid markers, a matrix concatenating all plastid markers, a matrix combining all plastid markers and ITS, and a matrix concatenating all plastid markers and ITS. For the ML and BI, we used the appropriate models of molecular evolution for each region using the corrected Akaike information criterion (AIC) and default search values for each region or marker, in jModeltest v2.1.7 (Darriba et al., 2012). Sequence matrix characteristics and evolution models used for phylogenetic analyses are shown in Table 1. ML analyses were performed using RAxML v8.1.2 (Stamatakis, 2014) with the following settings: rapid bootstrap analysis with 1000 replicates and search for best-scoring ML tree in one program run, starting with a random seed and *Arundinella nepalensis* Trin. as outgroup. Branches support was calculated by Bootstrap analysis. Bootstrap percentages (BP) are described as null (< 50), low (50–74 BP), moderate (75–84 BP) and high (85–100 BP). BI analysis was performed using MrBayes v3.2.5 (Ronquist et al., 2012; Ronquist & Huelsenbeck, 2003). BI analyses were conducted two independent runs of the Markov chain Monte Carlo (MCMC) for four million generations each and sampling one tree every 100 generations. We discarded the first 25% of each run as burn-in after checking for convergence and effective sample size (ESS > 200) in Tracer v1.6 (Drummond et al., 2012). The ESS values for each parameter of the run were greater than 200 after 4 million runs.

Divergence time estimates

To estimate divergence times of the *Imperata* clade, two time-calibrated ultrametric trees based on plastid

Table 1. Features of the DNA alignments used in the phylogenetic analyses.

D	A	N	NPI	NC	NV	NT	M
ndhF	BI	811	31 (3.8%)	721	87 (12%)	39	GTR + G + I
trnL-F	BI	1047	28 (2.6%)	834	105 (10%)	43	GTR + G
atpB-rbcL	BI	1005	31 (3%)	842	163 (16.2%)	42	GTR + G
ndhF + *trnL-F* + *atpB-rbcL*	ML	2855	93 (3.2%)	2388	303 (10.61%)	44	GTR + G + I
ITS	BI and ML	769	134 (17%)	510	248 (32.2%)	40	GTR + G
ndhF + *trnL-F* + *atpB-rbcL*+ ITS	ML	3625	227 (6.2%)	2898	551 (15.2%)	45	GTR + G + I

D: Data set; **A:** Phylogenetic analyses (BI: Bayesian inference; ML: Maximum likelihood); **N:** Total number of characters in data set; **NPI:** Number of parsimony informative sites; **NC:** number of constant characters; **NV:** Number of variable characters; **NT:** Number of terminals; **M:** Evolutionary model selected by AIC.

markers and ITS were estimated separately under a Bayesian approach as implemented in BEAST v1.10.4 (Suchard et al., 2018). Since there are no fossils of *Imperata* taxa that can be taken as calibration points, we used a secondary calibration date based on the dates estimated by Vicentini et al. (2008). The calibration of the origin of the grasses is controversial and varies depending on the type of fossil used (Prasad et al., 2005; Strömberg, 2005). Although Vicentini et al. (2008) expose different calibrations based on different types of fossils, we decided to use the youngest calibration, since it is congruent with other episodes such as low levels of atmospheric CO_2 and the expansion of C4 plants. We used the same dataset which we used for the phylogenetic analyses of concatenated plastid markers and ITS separately. The concatenated plastid and ITS analyses were rooted in *Arundinella nepalensis*. The node of the root was constrained using a normal prior distribution with a mean of 19.1 million years ago (Ma) and a standard deviation of 0.155 to represent the age range estimated by Vicentini et al. (2008). The two datasets were partitioned according to the best-fit models of evolution obtained with jModeltest v2.1.7 (Darriba et al., 2012), GTR + G + I for plastid markers and GTR + G for ITS. Analyses were run using a molecular clock model with uncorrelated rates, assuming a lognormal distribution of rates, and the Yule model as a tree prior (Gernhard, 2008). Two MCMC analyses were run each with 100 million generations and sampling every 10,000 generations. The time series plots of all parameters were analyzed in Tracer v1.6 (Drummond et al., 2012) to check for adequate ESS (ESS > 200) and convergence of the model's likelihood and parameters between each run. Trees were combined in Log Combiner v1.10.4 (Suchard et al., 2018), setting the burn-in at 25% of the initial samples of each MCMC run. Post-burn-in samples were summarized using the maximum clade credibility tree option in Tree Annotator v.1.10.4 (Suchard et al., 2018).

Study area and ecological niche modelling

We identified five *Imperata* lineages belonging to our phylogenetically recovered clade A for ecological niche modelling (ENM). Ecological niche model was applied to determine the potential distribution and quantify niche differentiation between the American lineages of *Imperata* using MaxEnt v3.4.1 (Phillips et al., 2006). The georeferenced points were obtained from field sampling carried out by us between the years 2017–2019 and from herbarium specimens collected from 1970 to the present. To avoid an autocorrelation spatial effect in the ENM, the points that were at distances of fewer than 50 km were eliminated using the R package 'Wallace' v1.0.6.1 (Kass et al., 2018) implemented in R v3.6.1. After filtering 212 localities, a total of 149 points was obtained for South America and 63 points for North America (Table S5, see supplemental material online). To characterize the environments, the environmental layers of 19 bioclimatic variables were obtained from the WorldClim 2 database (http://www.worldclim.org) at a resolution of 2.5 arc minute (Hijmans et al., 2005) and the layers of the soil of 8 edaphic variables from SoilGrids™ (https://www. isric. org), at a resolution of 250 m, and 5 cm deep (Hengl et al., 2017) (Table S6, see supplemental material online). In order to minimize biased fitting of the models produced by the covariance between variables, a correlation analysis was carried out to eliminate correlated environmental and edaphic variables using the PAST program v3.25 (Hammer et al., 2001). Therefore, we exclude variables with Pearson product-moment correlation coefficient exceeding pairs 0.8 (Table S7, see supplemental material online). We used Bio2 (Mean diurnal range), Bio6 (Min temperature of the coldest month), Bio8 (Mean temperature of the wettest quarter), Bio12 (Annual precipitation), Bio14 (Precipitation of the driest month), Bio15 (Precipitation seasonality), Bio18 (Precipitation of the warmest quarter), Bio19 (Precipitation of the coldest quarter), Bldfie (Bulk density), Clyppt (Clay content), Crfvol (Coarse fragments volumetric), Orcdrc (Soil organic carbon content), Phihox (Soil pH), Sltppt (Silt content) and Sndppt (Sand content) to model suitable areas in North and South America. Default settings were used for the MaxEnt run, including auto-features, a maximum of 500 iterations, and a maximum number of background points of 10,000, with a convergence threshold of 10^{-5}, and regularization multiplier 1. We used 75% random localities for model training and 25% for model testing by bootstrap with 10 replicates. The 10 models of each lineage were stored in ASCII raster format and imported to the QGIS 'Geographic Information System' Version 3.4.12 (2019) to produce a strict consensus map. The area under the 'receiver operating characteristic (ROC) curve' (AUC) (Elith & Leathwick, 2009; Peterson et al., 2008) values were used to evaluate the accuracy of each model prediction. Variable importance to ENMs was evaluated based on the permutation value, jackknife test and the response curves calculated by MaxEnt (Phillips et al., 2017).

Ecological niche overlap test

In order to assess the degree of niche overlap and to test the divergence or conservative niche hypothesis between the American lineages of *Imperata* defined

within clade A based on phylogenetic studies (the same lineages for which ecological niche modelling was performed), we applied a niche equivalence test (Identity test) and niche similarity test (Background test). We used ENM tools v1.3 (Warren et al., 2008, 2010) to calculate Schoener's D (Schoener, 1968) and standardized Hellinger distance (calculated as I) to measure niche overlap between lineages via pairwise comparison of lineages. The I and D values of the niche range from 0 (two species have no overlap in the environmental space) to 1 (two species share the same environmental space). We used the identity test to assess whether the ecological niches between lineages are equivalent (ecological niches are interchangeable), or significantly different ($p < 0.05$). A comparison of the experimental D and calculated I from each pair of lineages was made with a null distribution simulation of 100 pseudoreplicates generated by random sampling from data points pooled for each pair of lineages. The background test assesses whether the ecological niches of any pair of lineages are more different than expected by chance, and considers the environmental conditions available to them. Biotic regions serve as a reliable estimate of the area that is accessible to a species (Soberon & Peterson, 2005), so we chose as background the ecoregions where there are occurrences corresponding to each lineage. For this purpose, the world map of terrestrial ecoregions was used (Olson et al., 2001). A background test was performed using the locations of lineage 1 and random points (same number of locations) from the ecoregions where the lineage 2 locations occur. A null distribution was created with 100 pseudo-replicated values for each pair in both directions, and the experimental D and calculated I were compared. The overlap value between two ENMs was either above the 95% confidence interval of the null hypothesis, which supported niche conservatism, or below the 95% confidence interval of the null hypothesis, supporting the niche divergence.

Results

Phylogenetic analysis and divergence times of *Imperata* clade

The aligned data matrix, including the three plastid markers (*ndhF*, *trnL-F,* and *atpB-rbcL*) was 2855 base pairs long, of which 303 (10.61%) were variable and 93 (3.2%) were parsimony informative. The aligned ITS matrix was 510 base pairs long, of which 248 (32.2%) were variable and 134 (17%) were parsimony informative.

Combined and concatenated plastid analyses. The results of the combined and concatenated plastid markers analyses generated topologies in which all *Imperata* specimens form a well-supported clade (99 BS; 1 PP) as sister to a clade formed by the specimens belonging to the genera *Germainia* Balansa & Poitr, *Apocopis* Nees, and *Pogonatherum* P. Beauv. (92 BS; 1 PP) (Figs S1–S2, see supplemental material online). Within *Imperata* clade, some specimens belonging to the same taxon appear as supported lineages, but phylogenetic relationships between lineages are poorly supported. In the ML and BI trees, *I. minutiflora* (1, 2, and 3) (100 BS; 1 PP) and *I. brevifolia* (1 and 2) (79 BS; 1 PP) form lineages, respectively (Figs S1 and S2, see supplemental material online). In the ML tree, *I. condensata* (1 and 2) forms a lineage (75 BS) as sister to *I. brasiliensis* (1) (non-support) (Fig. S1, see supplemental material online). In the BI tree, *I. condensata* (1 and 2) forms a lineage (0.77 PP) within a clade formed by them and *I. brasiliensis* (1), *I. tenuis* (2) and *I. contracta* (0.7 PP); In the same tree, *I. brasiliensis* (2) and *I. tenuis* (1) form a lineage (0.82 PP) (Fig. S2, see supplemental material online).

ITS analyses. The results of the ITS analyses generated topologies in which the *Imperata* specimens form a well-supported clade (98 BS; 1 PP) separate into two clades (A and B) with moderate support (Figs S3–S4, see supplemental material online). Clade A (68 BS; 0.74 PP) groups the American specimens (*I. brasiliensis*, *I. brevifolia*, *I. condensata*, *I. contracta*, *I. minutiflora*, and *I. tenuis*) and clade B (61 BS; 0.8 PP) groups specimens from the rest of the world (*I. cheesemanii*, *I. conferta*, and *I. cylindrica*). Within clade A, some specimens belonging to the same taxon and some specimens belonging to different taxa appear as supported lineages, but phylogenetic relationships between lineages are poorly supported. In the ML tree within clade A, *I. minutiflora* (1, 2, and 3) forms a lineage (100 BS) as sister to a clade formed by *I. brasiliensis* (2), *I. condensata* (1 and 2), and *I. contracta* (non-support); In the same tree, within clade A, *I. brevifolia* (1 and 3) forms a lineage (96 BS) as sister to a clade formed by *I. brasiliensis* (1), *I. brasiliensis* (2), *I. tenuis* (1), and *I. tenuis* (2) (non-support) (Fig. S3, see supplemental material online). In the BI tree within clade A, *I. minutiflora* (1, 2, and 3) forms a lineage (1 PP) within a clade formed by them and *I. condensata* (1 and 2), I. *brasiliensis* (3), and *I. contracta* (0.74 PP); In the same tree, within clade A, *I. brevifolia* (1 and 3) forms a lineage (1 PP) (Fig. S4, see supplemental material online). In the ML and BI trees within clade A, *I. brasiliensis* (1 and 2) and *I. tenuis* (1 and 2) forms a lineage (55 BS; 0.9 PP) (Figs S3 and S4, see supplemental material online). In the

ML tree within clade B, *I. cheesemanii* (1 and 2) (72 BS), *I. conferta* (92 BS), *I. cylindrica* (2) (95 BS), and *I. cylindrica* (1) (61 BS) form separate lineages (Fig. S3, see supplemental material online). In the BI tree within clade B, *I. cheesemanii* (1 and 2) and *I. conferta* form a lineage (1 PP) (Fig. S4, see supplemental material online). In the same tree, *I. cylindrica* (2) (1 PP) and *I. cylindrica* (1) (0.8 PP) form separated lineages.

Combined and concatenated plastid and ITS analyses. The partition homogeneity test indicated that the combined plastid and ITS sequences ($p = 0.038$) were congruent, hence a combined analysis was performed to minimize sampling error and maximize the explanatory power of the data. The *Imperata* clade was highly supported (99 BS; 1.00 PP) and as sister to a clade formed by the taxa belonging to the genera *Germainia*, *Apocopis,* and *Pogonatherum* (77 BS; 1 PP) (Fig. 1). Within *Imperata* clade, clades A (67 BS; 0.83 PP) and B (82 BS; 0.73 PP) with moderate support were identified, which included specimens from America and the rest of the world, respectively. Within clade A, some specimens belonging to the same taxon and some specimens belonging to different taxa appear as supported lineages, but phylogenetic relationships between them are poorly supported. In the ML and BI trees within clade A, *I. brevifolia* (1, 2, and 3) forms a lineage (82 BS; 1 PP) (Fig. 1). In the ML tree within clade A, *I. brasiliensis* (2) and *I. tenuis* (1) form a lineage (92 BS) within a clade formed by them and *I. brasiliensis* (1) and *I. tenuis* (2) (non-support); In the same tree, within clade A, *I. minutiflora* (1, 2, and 3) form a lineage (100 BS) as sister to a clade formed by *I. condensata* (1 and 2) and *I. contracta* (60 BS), and *I. brasiliensis* (3) (non-support) (Fig. 1). In the BI tree within clade A, *I. brasiliensis* (1 and 2) and *I. tenuis* (1 and 2) form a lineage (0.7 PP); In the same tree, within clade A, *I. minutiflora* (1, 2, and 3) form a lineage (1 PP) and *I. condensata* (1 and 2) with *I. contracta* form other lineage (0.92 PP) (Fig. 1). In the ML tree within clade B, *I. cheesemanii* (1 and 2) (78 BS), *I. conferta* (94 BS), and *I. cylindrica* (2) (92 BS) form separate lineages (Fig. 1); In the same tree, *I. cylindrica* (1) form a lineage (50 BS) separated from clade A and B. In the BI tree, within clade B, *I. cheesemanii* (1 and 2) and *I. conferta* form a lineage (1 PP) (Fig. 1). In the same tree, *I. cylindrica* (2) (1 PP) and *I. cylindrica* (1) (0.75 PP) form separated lineages. Although *I. cylindrica* (1) appears separated from clade B in the ML analysis based on all the markers combined, we consider that its inclusion in it is supported by the results of the ML and BI analyses based on ITS (Figs S3–S4, see supplemental material online), in the BI analysis based on all the concatenated markers (Fig. 1) and the results of the dated ultrametric tree based on ITS (Fig. 2).

Although the specimens of *I. condensata* and *I. contracta* appear in a clade in the trees obtained in the analyses of all markers (Fig. 1), the specimens of *I. condensata* form a supported clade without *I. contracta* in the trees obtained in the analyses of all plastid markers (Figs S1 and S2, see supplemental material online) and the ultrametric dated tree based on plastid markers (Fig. 3). Furthermore, the position of *I. contracta* varies substantially between the trees obtained in the analyses of plastid and ITS separately, and the geographic distribution and ecological niche of both taxa differ enormously (see results of ecological niche modelling). For these reasons, we decided to treat *I. condensata* and *I. contracta* as separate lineages. In the case of *I. brasiliensis* and *I. tenuis*, since they form a supported clade in the trees obtained in the analyses of ITS (Figs S3 and S4, see supplemental material online), all markers (Fig. 1) and the ultrametric dated tree based on ITS (Fig. 3) (without including *I. brasiliensis* 3), and considering that the geographic distribution of both taxa overlaps, we decided to treat them as a single lineage. Considering the results of the phylogenetic analyses and the reasons given above, we decided to separate the American taxa of *Imperata* into five lineages as follows: *I. brasiliensis-I. tenuis*, *I. brevifolia*, *I. condensata*, *I. contracta* and *I. minutiflora*. These lineages were subsequently used for ecological niche modelling and ecological niche overlap analyses.

Regarding molecular dating, the phylogenetic resolution obtained with BEAST is greater than that obtained with Mr Bayes for both the plastid and ITS datasets. The chronogram obtained with the plastid markers (Fig. 3) gives an age of the beginning of *Imperata* diversification at 4.08 Ma (95% HDP 1.96-6.83). The chronogram obtained with the ITS dataset (Fig. 2) gives an age for the same event at 3.65 Ma (95% HDP 1.6-6.56). Although one is older than the other, both agree that the diversification of *Imperata* began in the Pliocene and that American lineages diverged during the Pleistocene-Holocene (From 2.56 Ma to the present).

Ecological niche models

We obtained the niche models that predict the potential distribution of *Imperata* lineages in South and North America (Fig. 4) based on the environmental variables that set the boundaries of the ecological niche. The AUC value indicated that all models had a high predictive ability, as it was > 0.9. The collection of points of occurrence of *I. brasiliensis-I. tenuis*, *I. contracta*, and *I. minutiflora* showed that these lineages occur in both

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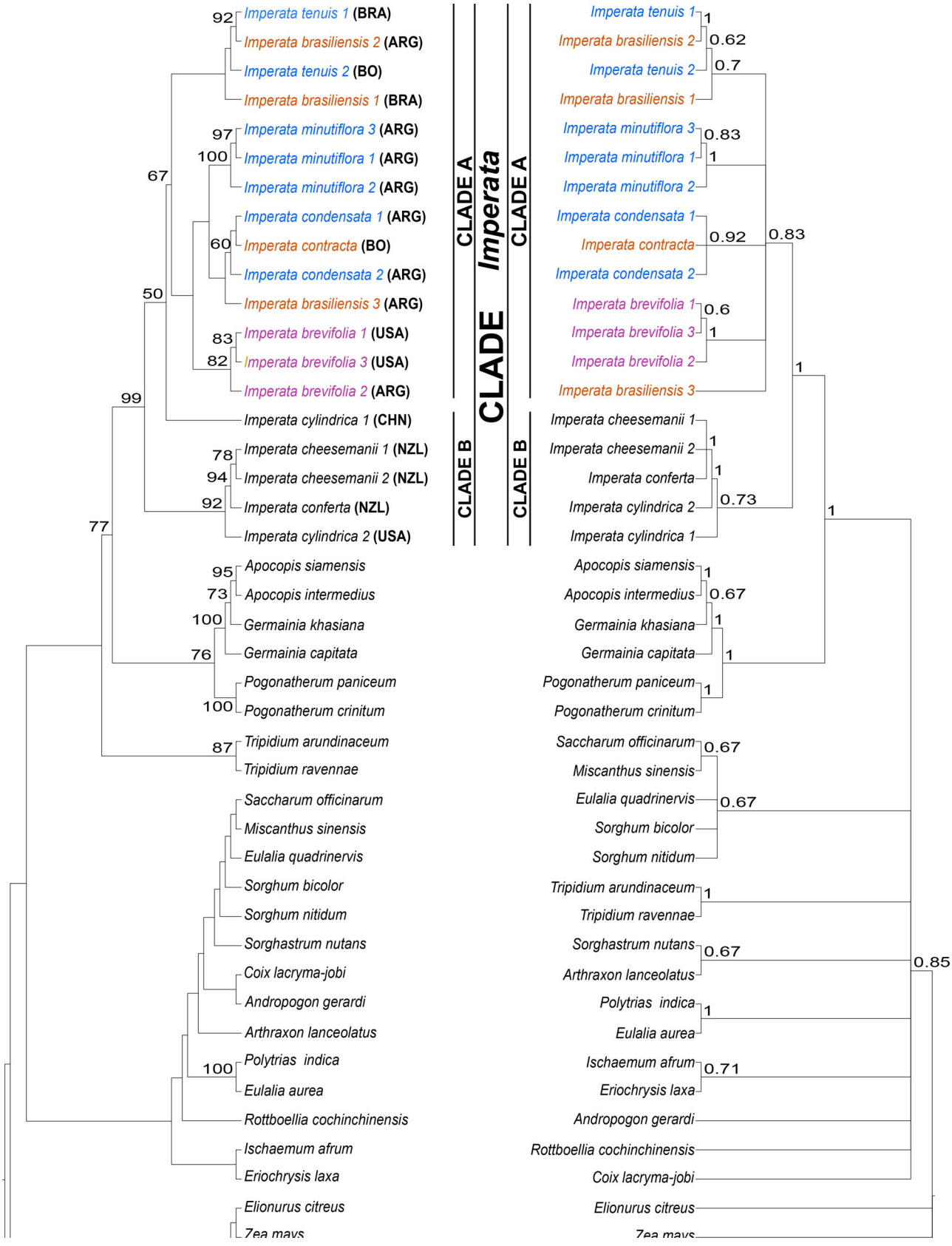

sympatry and allopatry. *Imperata brevifolia* and *I. condensata* occur in allopatry between them and with respect to the others. The climatic variables that contributed most in the MaxEnt models for *I. brasiliensis-I. tenuis* were the Bio6 (Min temperature of the coldest month), Bio12 (Annual precipitation), Bio14 (Precipitation of the driest month), and Bio18 (Precipitation of the warmest quarter) (Fig. S5, see supplemental material online). The area comprising the potential distribution of *I. brasiliensis-I. tenuis* is approximately 5,391,668 km^2. The potential distribution extends to some areas of Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, Paraguay, Peru, and Venezuela in South America, and the East coast of Mexico, and the southeast coast of the United States of America in North America. The potential distribution extends in areas where the coldest temperatures are around 10 °C (Bio6). Suitable areas showed annual precipitation values (Bio12) in the range 1,000-2,000 mm^3. With respect to the variables Bio14 and Bio18, suitable areas showed precipitation values in the range 50-100 mm^3 and 400-600 mm^3, respectively. The smallest potential distribution area was shown by *I. contracta*, comprising approximately 84,631 km^2. The potential distribution extends to some areas of Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, and Venezuela in South America, and the west and east coast of Mexico in North America. The Bio6, Bio15 (Precipitation seasonality), Bio18, and Bio 19 (Precipitation of the coldest quarter) were those variables that contributed most to the ENM model (Fig. S6, see supplemental material online). The potential distribution extends in areas where the coldest temperatures are around 25-30 °C (Bio6). Suitability was high in areas with high precipitation seasonality (Bio15). With respect to the variables Bio18 and Bio19, suitable areas showed precipitation values in the range 800-1,800 mm^3 and 2,000-2,500 mm^3, respectively. *Imperata minutiflora* showed the largest potential distribution comprising approximately 11,992,619 km^2. The potential distribution extends to some areas of Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru and Venezuela in South America, and the west and east coast of Mexico, and the south and southeast coast of the United States of America in North America. The variables Bio2 (Mean diurnal range), Bio6 and Bio18 contributed mainly to the ENM model (Fig. S7, see supplemental material online). Suitability was high in areas with low-temperature variation throughout the day (Bio2) and the potential distribution extends in areas where the coldest temperatures are around 5-20 °C (Bio6). Suitable areas showed precipitation values in the range 600-2,000 mm^3 (Bio18). The potential distribution of *I. condensata* comprised approximately 5,602,432 km^2. The potential distribution extends to some areas of Argentina, Bolivia, Chile, Colombia, Ecuador, and Peru in South America, and centre of Mexico, and west and south of the United States of America in North America. The Bio6, Bio15 and Bio18 were the variables that contributed mainly to ENM model (Fig. S8, see supplemental material online). The potential distribution extends in areas where the coldest temperatures are around −5-5 °C (Bio6). Suitability was high in areas with high precipitation seasonality (Bio15). Suitable areas showed precipitation values in the range 0-100 mm^3 (Bio18). The potential distribution of *I. brevifolia* comprised approximately 2,280,993 km^2. The potential distribution extends to some areas of Argentina, Bolivia, Chile, and Peru in South America, and north of Mexico and west coast of the United States of America in North America. The Bio6, Bio14 and Crfvol were the most important variables to predict its suitable ecological area (Fig. S9, see supplemental material online). The potential distribution extends in areas where the coldest temperatures are around −5-5 °C (Bio6). Suitable areas showed precipitation values in the range 0-25 mm^3 (Bio14). In addition, the suitability was high in areas with Crfvol high values.

Niche characteristics

With respect to the niche identity test, our results showed that the null hypothesis was rejected for some pairs of lineages, with the exception of pairs *I. brasiliensis-I. tenuis* with *I. minutiflora*, *I. contracta* with *I. minutiflora,* and *I. condensata* with *I. brevifolia* (Table 2), meaning that ENMs between these taxa were interchangeable and showing evidence of significant niche conservatism. The rejection of the null hypothesis in the equivalence test indicates that there is niche divergence between the pairs I. *brevifolia* and *I. condensata*, *I. brevifolia* and *I. minutiflora*, *I. brevifolia* and *I. brasiliensis-I. tenuis*, *I. condensata* and *I. minutiflora*, *I. condensata* and *I. contracta*, *I. condensata* and *I. brasiliensis-I. tenuis*, and *I.*

Fig. 1. Maximum likelihood (Left) and Bayesian inference (Right) trees of the *Imperata* clade, sister groups and outgroup based on plastid (*ndhF*, *atpB-rbcL*, *trnL-F*) and ITS. Maximum likelihood bootstrap values (≥50%) and Bayesian posterior probabilities (≥0.50) and are shown above branches. The *Imperata* clade consists of clades A and B. The colours represent where the taxa [according to Gabel (1982)] are present: South America (blue), North America (violet), or South and North America (orange). The initials in parentheses indicate the country of origin of the specimen: Argentina (ARG), Bolivia (BO), Brazil (BRA), China (CHN), New Zealand (NZL), and United States of America (USA).

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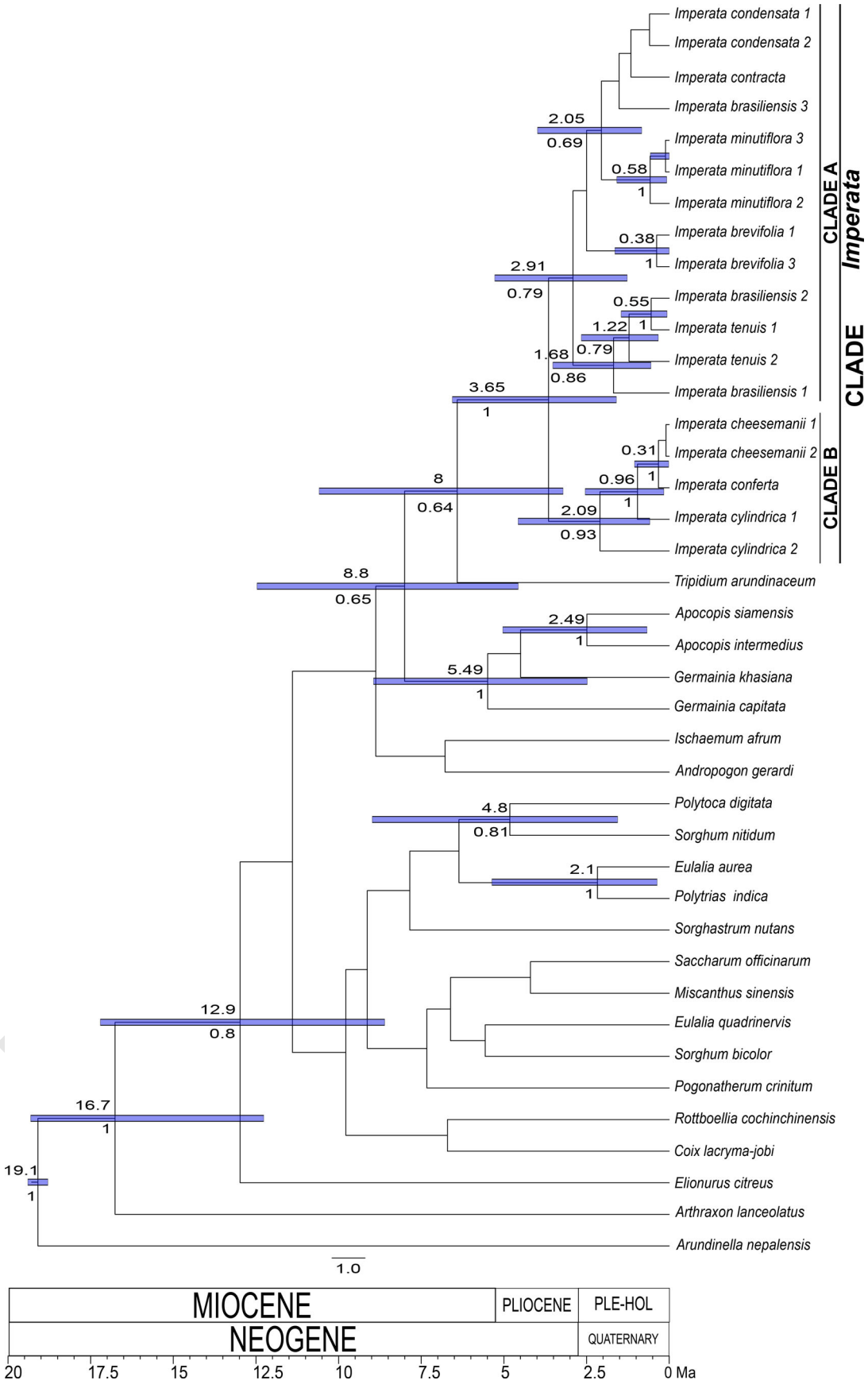

brasiliensis-I. tenuis and *I. contracta*. In the background test, the null hypothesis of the similarity test could not be rejected for some pairs of lineages, with the exception of the pairs *I. brasiliensis-I. tenuis* with *I. minutiflora*, *I. contracta* with *I. minutiflora* and *I. condensata* con *I. brevifolia* whose niche similarities were greater than those expected by chance, showing evidence of significant niche conservatism (Table 3). In addition, *I. condensata* with *I. minutiflora, I. contracta* with *I. brevifolia* and *I. brevifolia* with *I. minutiflora* also showed shared niche spaces that were more similar than expected by chance, but only in one direction. Opposite results were observed for reciprocal comparisons, since *I. brasiliensis-I. tenuis* were more similar to the environmental background surrounding occurrences of *I. brevifolia*, while this lineage showed fewer niche similarities than expected by chance in the opposite direction.

Discussion

Phylogenetic relationships of *Imperata*

Our results show clearly that *Imperata* is monophyletic within the tribe Adropogoneae and that it is formed by two clades that separate the American lineages from those of the rest of the world. Analysis with plastid markers recovers the close relationship of *Imperata* with other members of the subtribe Germainiinae (*Germainia*, *Apocopis, Pogonatherum*), which is consistent with previous studies (Estep et al., 2014; Lloyd Evans et al., 2019; Teerawatananon et al., 2011; Welker et al., 2016, 2020). The phylogenetic analysis of plastid markers and ITS separately has allowed us to establish which lineages within the clade *Imperata* were supported by each of the data sets. The joint analysis of plastid markers and ITS yielded a topology with better resolution than those obtained by analyzing each type of marker separately. From the trees generated in the ITS and combined analysis of all the markers, it is deduced that the taxa that inhabit in the Americas (Clade A) and those of the rest of the world (clade B) could have undergone different evolutionary paths, although the relationships between the lineages within clade A are unresolved. The use of inappropriate molecular markers and/or their low variability can cause low topological resolution in phylogenetic analyses (Whitfield & Lockhart, 2007). The polytomy observed in clade A in the BI analysis could be due to the low number of informative parsimony sites of the markers used, especially the plastid ones. On the other hand, polytomies in phylogenies may be due to rapid evolutionary radiation, resulting in simultaneous divergence events and evolutionary patterns that are not consistent with the presumption of a dichotomous branching tree (Hoelzer & Meinick, 1994; W. Maddison, 1989; Whitfield & Lockhart, 2007). There are antecedents in the Americas of rapid evolutionary radiation in Poaceae, such as the genus *Hordeum* L., which underwent rapid evolutionary radiation in North and South America during the Pleistocene associated with multiple geographical subdivisions (Glaubrecht & Schneider, 2010). It is possible that the polytomy observed in the clade A in the BI analysis may reflects a rapid species diversification process caused by geographic isolation as in *Hordeum*. Within the clade A, except *I. brasiliensis* and *I. tenuis*, the recovered lineages correspond to the taxa described by Gabel (1982). In plants there are examples of how introgression, hybridization, incomplete lineage sorting, or gene duplication (W. P. Maddison, 1997; Pamilo & Nei, 1988) affect phylogenetic reconstruction, causing contradictions between the delimitation of species based on molecular markers and morphological characters (Gurushidze et al., 2010; Jakob & Blattner, 2006; Li et al., 2016). According to the results of our phylogenetic analyses, the taxa described by Gabel (1982) as *I. brasiliensis* and *I. tenuis* may correspond to a single species. However, if *I. brasiliensis* and *I. tenuis* are considered different species according to the morphological characters used by Gabel (1982), and given that an extensive reticulate evolution has been documented among some members of the tribe Andropogoneae (Estep et al., 2014; Hodkinson et al., 2002; Skendzic et al., 2007), it cannot be ruled out that hybridization or introgression has occurred between *I. brasiliensis* and *I. tenuis* in the regions of South America where their distribution overlaps. We do not know why *I. brasiliensis* (3) does not appear in a clade along with the other specimens of *I. brasiliensis* and *I. tenuis*. Given that the morphological identification was correct and that the DNA sequencing presented good quality, we decided to include it in the analysis. However, it is possible that there was an error in the sequencing or that the specimen actually belongs to a different lineage with respect to the rest of the American lineages of *Imperata*.

Within clade B, the polytomy observed between *I. conferta* and *I. cheesemanii* in the trees obtained from the analysis of the ITS marker seems to be an artifact of

Fig. 2. Chronogram showing the evolutionary distances (in millions of years) between the species and accessions analyzed in the phylogenetic analysis of ITS. Node bars give the 95% highest posterior density (HPD) for the node height. The number above the bar indicates the mean age of the node in millions of years ago and the number below the bar indicates the posterior probability.

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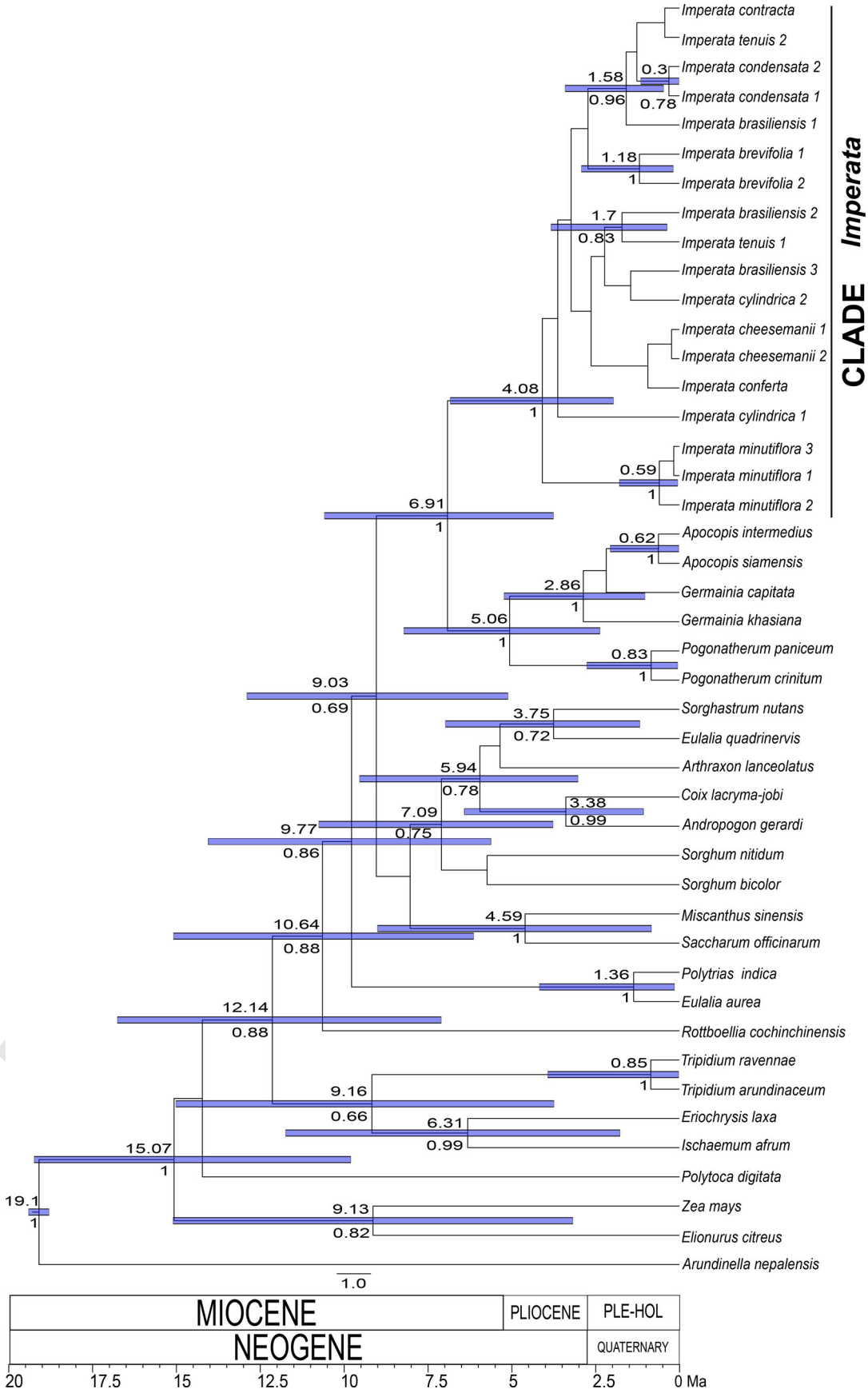

the BI analysis method, since in ML analysis with the same marker they form separate lineages that correspond to the taxonomy established by Gabel (1982). Specimens of *I. cylindrica* appear to be different lineages in the trees obtained from the analysis of the ITS marker. This could be related to the fact that some authors have reported different morphological varieties of *I. cylindrica* associated with different parts of the world (Gabel, 1982; Hubbard, 1944). Despite the results obtained, we suggest that a future exhaustive sampling of individuals and loci is required for a correct phylogenetic delimitation of the species within *Imperata*, especially the case of *I. brasiliensis* and *I. tenuis*.

EMN's of American *Imperata*

The importance of environmental variables in modelling and the potential distribution of each lineage was different, however in general it seems that *I. brevifolia* and *I. condensata* tolerate lower rainfall levels and lower temperatures than *I. brasiliensis-I. tenuis*, *I. contracta* and *I. minutiflora*. Our study has elucidated that the overlap and the differences observed in the current potential distributions of American lineages of *Imperata* based on environmental conditions are reflected in the niche overlap analyses. Concerning to ecological niche divergence tests, Warren et al. (2008) noted that when rejecting the niche equivalency null hypothesis, significant environmental niche differentiation occurs in association with speciation events. Additionally, they suggest that failure to reject the null hypothesis in the background test indicates that the data are such that there is insufficient power to make inferences regarding niche evolution. Our results of the identity and similarity test showed that the niches between some pairs of lineages are equivalent and similar, showing a clear phylogenetic niche conservatism, and between some pairs they are divergent. Regarding the result of the similarity test for *I. brasiliensis-I. tenuis* and *I. brevifolia*, the simplest explication of this counterintuitive result is that the environmental background of *I. brevifolia* appears to be so heterogeneous that the known locations of *I. brasiliensis-I. tenuis* look more similar to the known locations of *I. brevifolia* than its environmental background, even though their overall similarity is low. The phylogenetic niche conservatism (PNC) is the tendency of closely related lineages to retain ancestral ecological characteristics over time. If an environmental change occurred in the geographic space between populations of an ancestral species, isolation and allopatric speciation would happen if the populations conserve their niches and do not adapt to new ecological conditions (Kozak & Wiens, 2006; Wiens, 2004; Wiens & Graham, 2005). According to Kozak and Wiens (2006), if niche conservatism promotes allopatric speciation, the predicted distributions of a pair of sister species are expected to spatially overlap with each other but not with intervening locations where both species are absent. Given the results of the niche modelling and the niche overlap tests, the pair *I. brevifolia* and *I. condensata* could have experienced allopatric speciation promoted by niche conservatism, since there are no suitable areas between the potential geographic distribution of both lineages. Between these two lineages and the other American ones exist a niche divergence. The ecological niche divergence between related species can be a sign of ecological specialization (Shluter, 2001). The niche divergence between *I. brevifolia* and *I. condensata*, and the other lineages may be the result of an ecological speciation process promoted by adaptation and divergent selection. Lineages or species with overlapping geographic ranges may have undergone parapatric speciation or may have become parapatric after expanding their range after allopatric speciation occurred (Lynch, 1989). Such is the case of the pairs *I. brasiliensis-I. tenuis* with *I. minutiflora*, and *I. contracta* with *I. minutiflora.* They could have evolved by some mechanism of parapatric speciation, or have undergone allopatric speciation promoted by niche conservatism and have become parapatric by secondary contact. Respect the pair *I. brasiliensis-I. tenuis* and *I. contracta* seems to have had parapatric speciation but accompanied or promoted by niche divergence. As in other plants in America (Loera et al., 2012), it seems that the formation of different lineages or species of *Imperata* in the Neotropics during Quaternary is correlated with a combination of niche conservatism and niche divergence, both of which did or did not promote speciation.

Origin and expansion of *Imperata* in the neotropics

Based on the number of stamens and their distribution in Southeast Asia, Gabel (1982) suggested that *I. cylindrica* (or a similar ancestor) is probably the most ancestral specie in the genus. *Apocopis* and *Germainia*

Fig. 3. Chronogram showing the evolutionary distances (in millions of years) between the species and accessions analyzed in the phylogenetic analysis of the combined plastid markers. Node bars give the 95% highest posterior density (HPD) for the node height. The number above the bar indicates the mean age of the node in millions of years ago and the number below the bar indicates the posterior probability.

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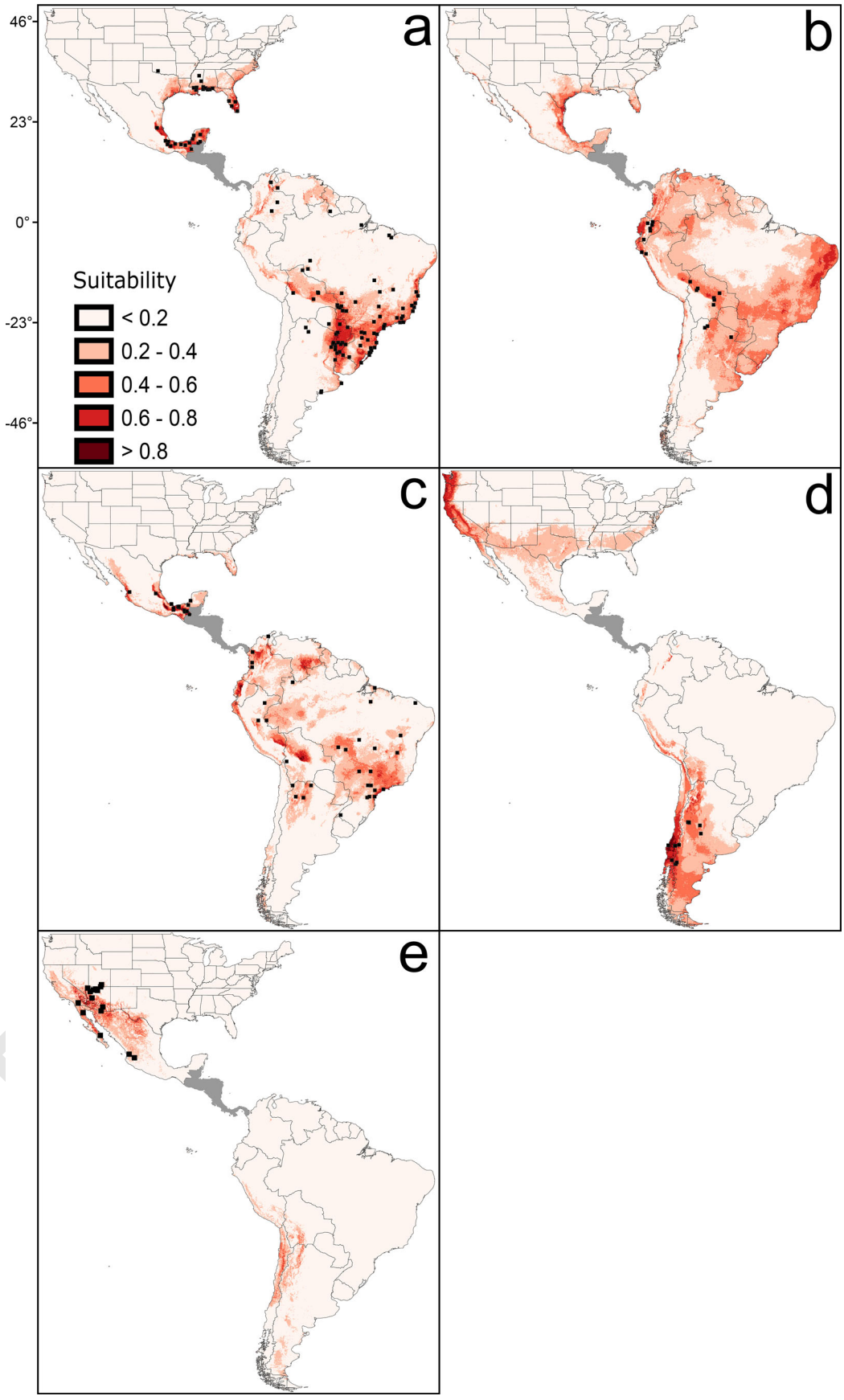

Table 2. Identity test of niche equivalency.

Taxa		Niche overlap		Niche equivalency (identity test)	
		D	I	D	I
I. brasiliensis – I. tenuis	*I. condensata*	0.2	0.84	Different **	Different **
	I. contracta	0.58	0.85	Different **	Different **
	I. brevifolia	0.08	0.24	Different **	Different **
	I. minutiflora	0.62	0.87	ns	ns
I. condensate	*I. contracta*	0.24	0.52	Different **	Different **
	I. brevifolia	0.57	0.81	ns	ns
	I. minutiflora	0.28	0.57	Different **	Different **
I. contracta	*I. brevifolia*	0.22	0.47	Different **	Different **
	I. minutiflora	0.69	0.91	ns	ns
I. brevifolia	*I. minutiflora*	0.19	0.44	Different **	Different **

A statistically significant value denotes a pair of species that are ecologically distinct (* $p \leq 0.05$, ** $p \leq 0.01$, ns $p > 0.05$). The niche overlap column shows the results of the metrics D and I obtained for each pair of taxa.

Table 3. Background test of niche similarity.

Taxa		Niche overlap		Niche similarity (background test)			
				D		I	
a	b	D	I	a → b	b → a	a → b	b → a
I. brasiliensis – I. tenuis	*I. condensata*	0.2	0.84	ns	ns	ns	ns
	I. contracta	0.58	0.85	ns	ns	ns	ns
	I. brevifolia	0.08	0.24	Similar*	Different**	Similar*	Different**
	I. minutiflora	0.62	0.87	Similar*	Similar**	Similar*	Similar**
I. condensata	*I. contracta*	0.24	0.52	ns	ns	ns	ns
	I. brevifolia	0.57	0.81	Similar**	Similar**	Similar**	Similar**
	I. minutiflora	0.28	0.57	Similar*	ns	Similar*	ns
I. contracta	*I. brevifolia*	0.22	0.47	Similar**	ns	Similar**	ns
	I. minutiflora	0.69	0.91	Similar**	Similar **	Similar**	Similar **
I. brevifolia	*I. minutiflora*	0.19	0.44	ns	Similar**	ns	Similar **

A statistically significant value denotes a pair of species that are ecologically distinct or similar (* $p \leq 0.05$, ** $p \leq 0.01$, ns $p > 0.05$). The niche overlap column shows the results of the metrics D and I obtained by comparing respective ENMS for each pair of taxa. Background test were performed between taxa in both directions, represented like a → b and b → a.

are distributed in India and Southeast Asia, such that it is possible that the ancestor of the subtribe Germainiinae likely lived in Southeast Asia. According to our results, the ancestral linage of *Imperata* and the other genera of the subtribe Germainiinae is dated at 6.91 Ma based on plastid markers (late Miocene), which coincides in time with the dispersion of other members of the tribe Andropogoneae from east Asia to other parts of the world (Estep et al., 2014; Welker et al., 2020). Ridley (1930) and Gabel (1982) suggested that *Imperata* reached the American continent by a long-distance dispersal event carried by animals, floating rhizomes, or by wind. Although several angiosperms have been scattered throughout the tropical Atlantic by long-distance dispersal (Martín-Bravo & Daniel, 2016; Renner, 2004; Tosso et al., 2018), we cannot deduce with our results neither the dispersion mode nor the starting point from where *Imperata* arrived in America. What we can suggest from our results is that American lineages come from a common ancestor. This ancestor of American *Imperata* lineages is dated in the late Pliocene based on ITS (2.91 Ma; 95% HDP 1.27-5.28). Since *Imperata* is distributed by the tropical and subtropical area of America, it is possible to consider that *Imperata* could have entered the continent through North, South, or Central America, spreading from there to other areas, as the Isthmus of Panama existed 3 Ma (Cody et al., 2010).

Fig. 4. Distribution of suitable niches of *Imperata* lineages. (a) *I. brasiliensis*-I. *tenuis*; (b) *I. minutiflora*; (c) *I. contracta*; (d) *I. condensata*; (e) *I. brevifolia*. The suitability value represents the predicted distribution probability (in logistic value) for current climatic conditions. Localities used in the ENM analysis marked as black squares. The area not included in the niche modelling is coloured grey.

As we indicated previously, a rapid process of species diversification caused by geographic isolation during the Quaternary, might be one of the reasons for the lack of phylogenetic resolution among the American *Imperata* lineages. In addition to allopatric divisions of populations resulting in different geographically separated species, ecological speciation of the lineages filling different niches constitute putative causes for rapid evolutionary radiation (Glaubrecht & Schneider, 2010). This type of rapid diversification in plants is generally associated with places where considerable climatic oscillations and/or geological events have occurred (C. Hughes & Eastwood, 2006; Richardson et al., 2001). Considering that the Quaternary period was characterized by climatic oscillations (Comes & Kadereit, 1998), the fact that the American *Imperata* lineages diverged during this period constitutes another potential indicator that there could have been a rapid divergence among American lineages. Under this scenario and considering the evaluation of ENMs based on the niche overlap performed in this study among American lineages of *Imperata*, rapid diversification would have been promoted by both ecological speciation, reflected in niche divergence, and/or allopatric speciation promoted by niche conservatism.

As future studies, we suggest an analysis of the historical biogeography of *Imperata* that explains the processes and events that have influenced on the dispersal around the planet and the evolution of the genus. Likewise, carry out phylogeographic analysis of the American *Imperata* species combined with paleo-modelling to delve deeper into the causes of the diversification of the genus in the Neotropics.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Supplemental data

Supplemental data for this article can be accessed here: https://dx.doi.org/10.1080/14772000.2021.1887959.

References

Alvarado-Sizzo, H., Casas, A., Parra, F., Arreola-Nava, H. J., Terrazas, T., & Sánchez, C. (2018). Species delimitation in the *Stenocereus griseus* (Cactaceae) species complex reveals a new species, *S. huastecorum*. *Public Library of Science One*, *13*, e0190385–25. https://doi.org/10.1371/journal.pone.0190385

Antonelli, A., Ariza, M., Albert, J., Andermann, T., Azevedo, J., Bacon, C., Faurby, S., Guedes, T., Hoorn, C., Lohmann, L. G., Matos-Maraví, P., Ritter, C. D., Sanmartín, I., Silvestro, D., Tejedor, M., ter Steege, H., Tuomisto, H., Werneck, F. P., Zizka, A., & Edwards, S. V. (2018). Conceptual and empirical advances in Neotropical biodiversity research. *PeerJ*, *6*, e5644–53. https://doi.org/10.7717/peerj.5644

Burke, S. V., Wysocki, W. P., Zuloaga, F. O., Craine, J. M., Pires, J. C., Edger, P. P., Mayfield-Jones, D., Clark, L. G., Kelchner, S. A., & Duvall, M. R. (2016). Evolutionary relationships in Panicoid grasses based on plastome phylogenomics (Panicoideae; Poaceae). *BioMed Central Plant Biology*, *16*, 1–11. https://doi.org/10.1186/s12870-016-0823-3

Cabido, M., Ateca, N., Astegiano, M. E., & Anton, A. M. (1997). Distribution of C3 and C4 grasses along an altitudinal gradient in Central Argentina. *Journal of Biogeography*, *24*, 197–204. https://doi.org/10.1046/j.1365-2699.1997.00085.x

Cavalli-Sforza, L. L., & Edwards, A. W. (1967). Phylogenetic analysis. Models and estimation procedures. *American Journal of Human Genetics*, *19*, 233–257. https://doi.org/10.2307/2406616

Clayton, W. D. (1972). The Awned Genera of Andropogoneae Studies in the Gramineae: XXXI. *Kew Bulletin*, *27*, 457. https://doi.org/10.2307/4114359

Clayton, W. D., & Renvoize, S. A. (1986). *Genera Graminum. Grasses of the world*. Bernan-Unipub.

Cody, S., Richardson, J. E., Rull, V., Ellis, C., & Pennington, R. T. (2010). The great American biotic interchange revisited. *Ecography*, *33*, 332. https://doi.org/10.1111/j.1600-0587.2010.06327.x

Comes, H. P., & Kadereit, J. W. (1998). The effect of quaternary climatic changes on plant distribution and evolution. *Trends in Plant Science*, *3*, 432–438. https://doi.org/10.1016/S1360-1385(98)01327-2

Coyne, J. A., Orr, A. H., & Orr, H. A. (2004). Species: Reality and concepts. *Speciation*. Sinauer Associates.

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). JModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772. https://doi.org/10.1038/nmeth.2109

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. https://doi.org/10.1093/molbev/mss075

Duan, L., Harris, A. J., Ye, W., Deng, S. W., Song, Z. Q., Chen, H. F., & Wen, J. (2019). Untangling the taxonomy of the Cladrastis clade (Leguminosae: Papilionoideae) by

integrating phylogenetics and ecological evidence. *TAXON*, *68*, 1189–1203. https://doi.org/10.1002/tax.12155

Edwards, E. J., Osborne, C. P., Strömberg, C. A. E., Smith, S. A., Bond, W. J., Christin, P.-A., Cousins, A. B., Duvall, M. R., Fox, D. L., Freckleton, R. P., Ghannoum, O., Hartwell, J., Huang, Y., Janis, C. M., Keeley, J. E., Kellogg, E. A., Knapp, A. K., Leakey, A. D. B., Nelson, D. M., … Tipple, B. (2010). The origins of C4 Grasslands: Integrating evolutionary and ecosystem science. *Science (New York, N.Y.)*, *328*, 587–591. https://doi.org/10.1126/science.1177216

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Estep, M. C., McKain, M. R., Vela Diaz, D., Zhong, J., Hodge, J. G., Hodkinson, T. R., Layton, D. J., Malcomber, S. T., Pasquet, R., & Kellogg, E. A. (2014). Allopolyploidy, diversification, and the Miocene grassland expansion. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 15149–15154. https://doi.org/10.1073/pnas.1404177111

Farris, J. S., Källersjö, M., Kluge, A. G., & Bult, C. (1995). Constructing a significance test for incongruence. *Systematic Biology*, *44*, 570–572. https://doi.org/10.1093/sysbio/44.4.570

Felsenstein, J. (1981). Evolutionary trees from DNA sequences: A maximum likelihood approach. *Journal of Molecular Evolution*, *17*, 368–376. https://doi.org/10.1007/BF01734359

Gabel, M. L. (1982). A biosystematic study of the genus Imperata (Gramineae: Andropogoneae) https://doi.org/10.31274/rtd-180813-5836

Q5 Gernhard, T. (2008). The conditioned reconstructed process. *Journal of Theoretical Biology*, *253*, 769–778. https://doi.org/10.1016/j.jtbi.2008.04.005

Giudicelli, G. C., Turchetto, C., Silva-Arias, G. A., & Freitas, L. B. (2019). Influence of climate changes on the potential distribution of a widespread grassland species in South America. *Perspectives in Plant Ecology, Evolution and Systematics*, *41*, 125496. https://doi.org/10.1016/j.ppees.2019.125496

Givnish, T. J. (2010). Ecology of plant speciation. *TAXON*, *59*, 1326–1366. https://doi.org/10.1002/tax.595003

Glaubrecht, M., & Schneider, H. (2010). Evolution in action: Case studies in adaptive radiation, speciation and the origin of biodiversity. https://doi.org/10.1007/978-3-642-12425-9

Q6 Graham, C. H., Ron, S. R., Santos, J. C., Schneider, C. J., & Moritz, C. (2004). Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution; International Journal of Organic Evolution*, *58*, 1781–1793. https://doi.org/10.1111/j.0014-3820.2004.tb00461.x

Grass Phylogeny Working Group II. (2012). New grass phylogeny resolves deep evolutionary relationships and discovers C4 origins. *New Phytologist*, *193*, 304–312. https://doi.org/10.1111/j.1469-8137.2011.03972.x

Gurushidze, M., Fritsch, R. M., & Blattner, F. R. (2010). Species-level phylogeny of Allium subgenus Melanocrommyum: Incomplete lineage sorting, hybridization and trnF gene duplication. *TAXON*, *59*, 829–840. https://doi.org/10.1002/tax.593012

Hall, T. A. (1999). BIOEDIT: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*.

Q7 Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). Past: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*.

Q8 Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S., & Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *Public Library of Science One*, *12*, e0169748. https://doi.org/10.1371/journal.pone.0169748

Hennig, W. (1966). *Phylogenetic systematics*. University of Illinois Press.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). WorldClim. Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/joc.1276

Hodkinson, T. R., Chase, M. W., Lledó, M. D., Salamin, N., & Renvoize, S. A. (2002). Phylogenetics of Miscanthus, Saccharum and related genera (Saccharinae, Andropogoneae, Poaceae) based on DNA sequences from ITS nuclear ribosomal DNA and plastid trnLintron and trnL-F intergenic spacers . *Journal of Plant Research*, *115*, 381–392. https://doi.org/10.1007/s10265-002-0049-3

Hoelzer, G. A., & Meinick, D. J. (1994). Patterns of speciation and limits to phylogenetic resolution. *Trends in Ecology & Evolution*, *9*, 104–107. https://doi.org/10.1016/0169-5347(94)90207-0

Hubbard, C. E. (1944). Taxonomy, description and distribution of species and varieties. In *Imperata Cylindrica Taxonomy, Distribution, Economic Significance and Control. Imperial Agricultural Bureaux Joint Publ. 7*.

Hughes, C., & Eastwood, R. (2006). Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 10334–10339. https://doi.org/10.1073/pnas.0601928103

Hughes, C. E., Pennington, R. T., & Antonelli, A. (2013). Neotropical plant evolution: Assembling the big picture. *Botanical Journal of the Linnean Society*, *171*, 1–18. https://doi.org/10.1111/boj.12006

Jakob, S. S., & Blattner, F. R. (2006). A chloroplast genealogy of Hordeum (Poaceae): Long-term persisting haplotypes, incomplete lineage sorting, regional extinction, and the consequences for phylogenetic inference. *Molecular Biology and Evolution*, *23*, 1602–1612. https://doi.org/10.1093/molbev/msl018

Kass, J. M., Vilela, B., Aiello-Lammens, M. E., Muscarella, R., Merow, C., & Anderson, R. P. (2018). Wallace: A flexible platform for reproducible modeling of species niches and distributions built for community expansion. *Methods in Ecology and Evolution*, *9*, 1151–1156. https://doi.org/10.1111/2041-210X.12945

Katoh, K., Rozewicki, J., & Yamada, K. D. (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics*, *20*, 1160–1166. https://doi.org/10.1093/bib/bbx108

Kellogg, E., & Kubitzki, K. (2015). *Flowering Plants. Monocots: Poaceae*.

Khanuja, S., Shasany, A., Darokar, M. P., & Kumar, S. (1999). Rapid isolation of DNA from dry and fresh samples of plants producing large amounts of secondary metabolites and essential oils. *Plant Molecular Biology Reporter*, *17*, 74–74. https://doi.org/10.1023/A:1007528101452

Kirschner, J. A., & Hoorn, C. (2020). The onset of grasses in the Amazon drainage basin, evidence from the fossil record. *Frontiers of Biogeography*, *12*. https://doi.org/10.21425/F5FBG44827

Kozak, K. H., & Wiens, J. J. (2006). Does niche conservatism promote speciation? A case study in North American Salamanders. *Evolution; International Journal of Organic Evolution*, *60*, 2604–2621. https://doi.org/10.1554/06-334.1

Larsson, A. (2014). AliView: A fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics (Oxford, England)*, *30*, 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Leavitt, S. D., Moreau, C. S., & Thorsten Lumbsch, H. (2015). The dynamic discipline of species delimitation: Progress toward effectively recognizing species boundaries in natural populations. In D. K. Upreti, P. K. Divakar, V. Shukla, & R. Bajpai (Eds.), *Recent advances in lichenology: Modern methods and approaches in lichen systematics and culture techniques* (Vol. 2, pp. 11–44), Springer India. https://doi.org/10.1007/978-81-322-2235-4_2

Li, Q. Q., Zhou, S. D., Huang, D. Q., He, X. J., & Wei, X. Q. (2016). Molecular phylogeny, divergence time estimates and historical biogeography within one of the world's largest monocot genera. *AoB Plants*, *8*, plw041. https://doi.org/10.1093/aobpla/plw041

Lloyd Evans, D., Joshi, S. V., & Wang, J. (2019). Whole chloroplast genome and gene locus phylogenies reveal the taxonomic placement and relationship of Tripidium (Panicoideae: Andropogoneae) to sugarcane. *BioMed Central Evolutionary Biology*, *19*, 1–20. https://doi.org/10.1186/s12862-019-1356-9

Loera, I., Sosa, V., & Ickert-Bond, S. M. (2012). Diversification in North American arid lands: Niche conservatism, divergence and expansion of habitat explain speciation in the genus Ephedra. *Molecular Phylogenetics and Evolution*, *65*, 437–450. https://doi.org/10.1016/j.ympev.2012.06.025

Lynch, J. D. (1989). The gauge of speciation: on the frequencies of modes of speciation.In D. Otte & J. A. Endler (Eds.), *Speciation and its consequences* (pp. 527–553). Sinauer.

Maddison, W. (1989). Reconstructing character evolution on polytomous cladograms. *Cladistics*, *5*, 365–377. https://doi.org/10.1111/j.1096-0031.1989.tb00569.x

Maddison, W. P. (1997). Gene trees in species trees. *Systematic Biology*, *46*, 523–536. https://doi.org/10.1093/sysbio/46.3.523

Martín-Bravo, S., & Daniel, T. F. (2016). Molecular evidence supports ancient long-distance dispersal for the amphi-atlantic disjunction in the giant yellow shrimp plant (Barleria oenotheroides). *American Journal of Botany*, *103*, 1103–1116. https://doi.org/10.3732/ajb.1600083

Mathews, S., Spangler, R. E., Mason Gamer, R. J., & Kellogg, E. A. (2002). Phylogeny of Andropogoneae Inferred from Phytochrome B, GBSSI, and ndhF. *International Journal of Plant Sciences*, *163*, 441–450. https://doi.org/10.1086/339155

Mau, B., Newton, M. A., & Larget, B. (1999). Bayesian phylogenetic inference via Markov chain Monte Carlo methods. *Biometrics*, *55*, 1–12. https://doi.org/10.1111/j.0006-341x.1999.00001.x

Mayden, R. L. (1999). Consilience and a hierarchy of species concepts: Advances toward closure on the species puzzle. *Journal of Nematology*, *31*, 95–116.

Morrone, J. J. (2014). Cladistic biogeography of the Neotropical region: Identifying the main events in the diversification of the terrestrial biota. *Cladistics*, *30*, 202–214. https://doi.org/10.1111/cla.12039

Nakazato, T., Warren, D. L., & Moyle, L. C. (2010). Ecological and geographic modes of species divergence in wild tomatoes. *American Journal of Botany*, *97*, 680–693. https://doi.org/10.3732/ajb.0900216

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, *51*, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2 https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA2.0.CO;2]

Pamilo, P., & Nei, M. (1988, July). Relationships between gene trees and species trees. *Molecular Biology and Evolution*, *5*, 568–583. https://doi.org/10.1093/oxfordjournals.molbev.a040517

Pelser, P. B., Kennedy, A. H., Tepe, E. J., Shidler, J. B., Nordenstam, B., Kadereit, J. W., & Watson, L. E. (2010). Patterns and causes of incongruence between plastid and nuclear Senecioneae (Asteraceae) phylogenies. *American Journal of Botany*, *97*, 856–873. https://doi.org/10.3732/ajb.0900287

Peterson, A. T., Papeş, M., & Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, *213*, 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*, 887–893. https://doi.org/10.1111/ecog.03049

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Prasad, V., Strömberg, C. A. E., Alimohammadian, H., & Sahni, A. (2005). Paleontology: Dinosaur coprolites and the early evolution of grasses and grazers. *Science*, *310*, 1177–1180. https://doi.org/10.1126/science.1118806

Rannala, B., & Yang, Z. (1996). Probability distribution of molecular evolutionary trees: A new method of phylogenetic inference. *Journal of Molecular Evolution*, *43*, 304–311. https://doi.org/10.1007/BF02338839

Renner, S. (2004). Plant dispersal across the tropical Atlantic by wind and sea currents. *International Journal of Plant Sciences*, *165*, S23–S33. https://doi.org/10.1086/383334

Richardson, J. E., Pennington, R. T., Pennington, T. D., & Hollingsworth, P. M. (2001). Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science (New York, N.Y.)*, *293*, 2242–2245. https://doi.org/10.1126/science.1061421

Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics (Oxford, England)*, *19*, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Ronquist, F., van der Mark, P., & Huelsenbeck, J. P. (2012). Bayesian phylogenetic analysis using MRBAYES. In *The*

phylogenetic handbook. https://doi.org/10.1017/cbo9780511819049.009

Ruiz-Sanchez, E., & Sosa, V. (2010). Delimiting species boundaries within the Neotropical bamboo Otatea (Poaceae: Bambusoideae) using molecular, morphological and ecological data. *Molecular Phylogenetics and Evolution*, *54*, 344–356. https://doi.org/10.1016/j.ympev.2009.10.035

Schluter, D. (2001). Ecology and the origin of species. *Trends in Ecology & Evolution*, *16*, 372–380. https://doi.org/10.1016/S0169-5347(01)02198-X

Schoener, T. W. (1968). The Anolis Lizards of Bimini: Resource partitioning in a complex fauna. *Ecology*, *49*, 704–726. https://doi.org/10.2307/1935534

Shao, Y. Z., Chen, Y., Zhang, X. C., & Xiang, Q. P. (2020). Species delimitation and phylogeography of Abies delavayi complex: Inferred from morphological, molecular, and climatic data. *Journal of Systematics and Evolution*, *58*, 234–246. https://doi.org/10.1111/jse.12500

Skendzic, E., Columbus, T., & Cerros-Tlatilpa, R. (2007). Phylogenetics of Andropogoneae (Poaceae: Panicoideae) based on nuclear ribosomal internal transcribed spacer and chloroplast trnL–F sequences. *Aliso*, *23*, 530–544. https://doi.org/10.5642/aliso.20072301.40

Soberon, J., & Peterson, A. T. (2005, January). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*. https://doi.org/10.17161/bi.v2i0.4

Soreng, R. J., Peterson, P. M., Romaschenko, K., Davidse, G., Teisher, J. K., Clark, L. G., Barberá, P., Gillespie, L. J., & Zuloaga, F. O. (2017). A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. *Journal of Systematics and Evolution*, *55*, 259–290. https://doi.org/10.1111/jse.12262

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics (Oxford, England)*, *30*, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Strömberg, C. A. E. (2005). Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 11980–11984. https://doi.org/10.1073/pnas.0505700102

Strömberg, C. A. E. (2011). Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences*, *39*, 517–544. https://doi.org/10.1146/annurev-earth-040809-152402

Su, X., Wu, G., Li, L., & Liu, J. (2015). Species delimitation in plants using the Qinghai-Tibet Plateau endemic Orinus (Poaceae: Tridentinae) as an example. *Annals of Botany*, *116*, 35–48. https://doi.org/10.1093/aob/mcv062

Suchard, M. A., Lemey, P., Baele, G., Ayres, D. L., Drummond, A. J., & Rambaut, A. (2018). Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution*, *4*, vey016 https://doi.org/10.1093/ve/vey016

Swofford, D. L. (2002). Phylogenetic analysis using Parsimony Version 4.0 beta version. Sinauer Associates.

Teerawatananon, A., Jacobs, S. W. L., & Hodkinson, T. R. (2011). Phylogenetics of Panicoideae (Poaceae) based on chloroplast and nuclear DNA sequences. *Telopea*, *13*, 115–142. https://doi.org/10.7751/telopea20116009

Thiers, B. (2020). *Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff*. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/

Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, *22*, 4673–4680. https://doi.org/10.1093/nar/22.22.4673

Tosso, F., Hardy, O. J., Doucet, J. L., Daïnou, K., Kaymak, E., & Migliore, J. (2018). Evolution in the Amphi-Atlantic tropical genus Guibourtia (Fabaceae, Detarioideae), combining NGS phylogeny and morphology. *Molecular Phylogenetics and Evolution*, *120*, 83–93. https://doi.org/10.1016/j.ympev.2017.11.026

Vicentini, A., Barber, J. C., Aliscioni, S. S., Giussani, L. M., & Kellogg, E. A. (2008). The age of the grasses and clusters of origins of C4 photosynthesis. *Global Change Biology*, *14*, 2963–2977. https://doi.org/10.1111/j.1365-2486.2008.01688.x

Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution; International Journal of Organic Evolution*, *62*, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Warren, D. L., Glor, R. E., & Turelli, M. (2010). ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography*, *33*, 607–611. https://doi.org/10.1111/j.1600-0587.2009.06142.x

Welker, C. A. D., McKain, M. R., Estep, M. C., Pasquet, R. S., Chipabika, G., Pallangyo, B., & Kellogg, E. A. (2020). Phylogenomics enables biogeographic analysis and a new subtribal classification of the Andropogoneae (Poaceae – Panicoideae). *Journal of Systematics and Evolution*, *58*, 1003–1001. https://doi.org/10.1111/jse.12691

Welker, C. A. D., Souza-Chies, T. T., Longhi-Wagner, H. M., Peichoto, M. C., McKain, M. R., & Kellogg, E. A. (2015). Phylogenetic analysis of Saccharum S.L. (Poaceae; Andropogoneae), with emphasis on the circumscription of the south American species. *American Journal of Botany*, *102*, 248–263. https://doi.org/10.3732/ajb.1400397

Welker, C. A. D., Souza-Chies, T. T., Longhi-Wagner, H. M., Peichoto, M. C., McKain, M. R., & Kellogg, E. A. (2016). Multilocus phylogeny and phylogenomics of Eriochrysis P. Beauv. (Poaceae-Andropogoneae): Taxonomic implications and evidence of interspecific hybridization. *Molecular Phylogenetics and Evolution*, *99*, 155–167. https://doi.org/10.1016/j.ympev.2016.02.022

Whitfield, J. B., & Lockhart, P. J. (2007). Deciphering ancient rapid radiations. *Trends in Ecology & Evolution*, *22*, 258–265. https://doi.org/10.1016/j.tree.2007.01.012

Wiens, J. J. (2004). Speciation and Ecology revisited: Phylogenetic niche conservatism and the origin of species. *Evolution; International Journal of Organic Evolution*, *58*, 193–197. https://doi.org/10.1554/03-447

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, *36*, 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

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