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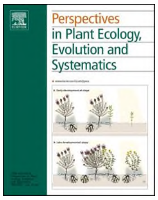

Geographic distribution and climatic niche comparison between diploid and polyploid cytotypes of a South American genus *Lessingianthus* H.Rob. (Vernonieae, Asteraceae)

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ABSTRACT

The distribution of ploidy levels and their ecological associations were studied using the genus *Lessingianthus* (Vernonieae, Asteraceae) as a model system. This genus is very complex from a cytogenetic point of view, with high cytotype diversity at the interspecific and intraspecific levels and with a continuous distribution throughout South America. So far, no previous studies have summarized chromosome count data for *Lessingianthus* or addressed the cytogeography of the genus. In this study, the ploidy levels of *Lessingianthus* species were determined by chromosome counts during mitosis and ecological niche modelling (ENM) was used to compare the environmental associations of the diploid and polyploid cytotypes. In total, 28 chromosome counts and six ploidy levels ($2x$, $4x$, $6x$, $8x$, $10x$, and $11x$) were recorded. Among these counts, the chromosome numbers for three hexaploids with $2n = 96$ (*L. parvifolius*, *L. vepretorum* and *L.* "bolivianensis" sp. ined.) and one decaploid taxon with $2n = 160$ (*L. roseus*) were reported for the first time. In addition, a new cytotype for *L. laniferus* ($2n = 6x = 96$) was also reported. The cytogeographic analysis resulted in detecting two geographic zones with high diversity of cytotypes and species. The ENMs showed that the areas of climatic suitability of diploids and polyploids are similar in extent, as well as the climatic requirements, showing high values of niche overlap within the environmental space. Our findings suggested that polyploidization in *Lessingianthus* has not caused expansion to novel environmental conditions and phylogenetic niche conservatism (PNC) may explain the lack of niche differentiation between diploids and polyploids.

1. Introduction

Polyploidy or whole genome duplication (WGD) is a common phenomenon in plants and it has played an important role in their evolution (Soltis et al., 2015; Stebbins, 1950; Van de Peer et al., 2017). One of the important consequences of WGD is the possibility of evolving duplicated copies of genes to fulfil new or slightly varied functions (neo-functionalisation or subfunctionalisation of genes) (Blanc and Wolfe, 2004; Cusack and Wolfe, 2007).

Under an adaptive evolutionary scenario such changes can result in organisms taking advantage of new ecological opportunities or facing new environmental challenges (Fawcett et al., 2013; Ohno, 1970; Schranz et al., 2012). Several studies have shown that in species with different ploidy, the cytotypes may have different ecological requirements (Mairal et al., 2018; Rojas-Andrés et al., 2020; Solís Neffa et al., 2022). However, other studies have not detected any habitat differentiation between the cytotypes (Castro et al., 2018, 2019; Glennon et al., 2014; Marchant et al., 2016; Via do Pico et al., 2019; Visser and Molofsky, 2015). The lack of ecological niche differentiation between cytotypes may be due to various reasons. Ecological divergence may arise over time and new cytotypes may not have had enough time to diverge (Godsoe et al., 2013; Schranz et al., 2012). The distribution of cytotypes may also depend on their origin either by autopolyploidy (intraspecific genomic duplication) or allopolyploidy (interspecific amalgamation of genomes through the combined processes of hybridization and genome duplication) (Soltis and Soltis, 1999, 2012). Allopolyploidy may be related to more pronounced niche shifts, because allopolyploids (with their fixed heterozygosity) may be more successful

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in colonizing difficult habitats than their parents, leading to latitudinal or elevational gradients in polyploid richness (Abbott and Brochmann, 2003; Brochmann et al., 2004). Alternatively, environmental conditions may reduce competition between parents by opening up new niches or ranges, allowing immediate colonization with considerable niche conservatism between the allopolyploids and their parents (Marchant et al., 2016). If we consider that polyploid species are closely related to their diploid parents, they may therefore exhibit phylogenetic niche conservatism (PNC). PNC implies that phylogenetically related taxa are likely to occupy more similar environments (Losos, 2008), which could lead to a lack of ecological niche differentiation between different ploidy levels. One of the methods used to test PNC is through ecological niche modeling (ENM) (Elith et al., 2006; Pyron et al., 2015). From the ecological niche models of a set of species, the variation between them can be assessed with respect to each other and the available niche volume where they occur (Pearson and Dawson, 2003). These tests can be used to assess PNC in related species in adjacent areas, and to assess the ecological divergence across landscapes (Broennimann et al., 2012; Glor and Warren, 2011).

ENM is a valuable tool that can be used with different approaches; it has been used to assess the niche shift hypothesis in related diploid-polyploid species (Glennon et al., 2012; McIntyre, 2012; Oberprieler et al., 2012; Visger et al., 2016) or in the analysis of different cytotypes within a species (Castro et al., 2019; Godsoe et al., 2013). Studies of this type are especially interesting in species with multiple ploidy levels, a wide distribution, living in adjacent areas, and that occur in heterogeneous environments. A good model for studying several of these aspects is the South American genus *Lessingianthus* H.Rob. (Vernonieae, Asteraceae), which includes 133 species (Angulo and Dematteis, 2016), characterized by herbaceous perennials or shrubs with xylopodium, having medium or large-sized heads grouped in seriate-cymose synflorescences, and pollen type “B” (Angulo and Dematteis, 2010; Robinson, 1999). The species are mainly distributed in Brazil, Paraguay, Argentina, and Bolivia, with some species extending into Uruguay, Colombia, Venezuela, and Peru (Robinson, 1999). Most species have a wide geographic distribution and they live in adjacent areas, although there are some endemic taxa, such as *L. profusus* (Dematt. and Cabrera) M. B. Angulo, *L. centauropsideus* (Hieron.) Dematt. and *L. teyucuarensis* (Cabrera) Dematt.

Lessingianthus species are found in diverse habitats growing mainly in *campo cerrado* (an open scrubland (3–6 m tall) with few trees, according to Cardoso Da Silva et al., 2002) and *campo rupestres* (a mosaic habitat characterized by quartzite substrates and supporting grassland and scrub, according to Mucina, 2018) (Robinson, 2009). However, some species grow in low fields with flooded soils (Dematteis, 2004). In addition to all this great ecological variability, polyploidy is one of the most prominent characteristics of the genus (Angulo, 2012; Angulo and Dematteis, 2009a; b, 2010, 2012a, b, 2015; Dematteis, 1997, 2002, 2009; Dematteis and Fernández, 2000; Dematteis et al., 2007). Ploidy levels of species ranging from diploid ($2n = 2x = 32$) to undecaploid ($2n = 11x = 176$) are all based on $x = 16$ (Angulo and Dematteis, 2012a).

The genus has the highest proportion of polyploid taxa known (70% of a total of 40 taxa analyzed so far, Angulo and Dematteis, 2012a) in the tribe Vernonieae. In addition to the large variation in the chromosome numbers observed, *Lessingianthus* also shows chromosome intraspecific variation and also has species with different ploidy levels, such as *L. laniferus* (Cristóbal & Dematt.) M.B. Angulo, *L. rubricaulis* (Humb. & Bonpl.) H.Rob. and *L. sellowii* (Less.) H.Rob. (Angulo and Dematteis, 2009b, 2012a). On the other hand, several "polyploid complexes'' were reported, which are formed by related species that are morphologically similar but have different ploidy levels (*L. rubricaulis* and *L. saltensis* (Hieron.) H.Rob.) (Angulo and Dematteis, 2009a, 2012b), which makes their study even more interesting. Therefore, the great diversity of cytotypes observed and the wide geographical distribution of the group will allow us to assess whether the polyploidization events observed for the genus have led to ecological differentiation.

In this scenario, the aims of the present study are: (1) to increase the cytological records for the species, by providing unpublished chromosome numbers (2) to present a review of all the vouchers of published counts (3) to determine the frequencies of different cytotypes of the genus (4) to establish the distribution of different ploidy levels in South American ecoregions and (5) to determine whether diploid and polyploid cytotypes have different ecological associations that could explain their geographical distributions.

2. Materials and methods

2.1. Material

The cytological studies were carried out with seeds collected from natural populations from different localities in Argentina, Bolivia, Brazil, Paraguay, and Uruguay, during 2005–2019. The specimens collected were deposited in the herbarium of the Instituto de Botánica del Nordeste (CTES) Corrientes, Argentina.

2.2. Chromosome counts

Mitotic chromosome preparations made from root tips of germinating seeds were pretreated in 0.002 M 8-hydroxyquinoline for 4–5 h, then fixed in acetic acid: absolute alcohol (3:1) overnight and stored in 70% aqueous ethanol. The root tips were stained according to the Feulgen technique and the meristems were macerated and squashed in a drop of lacto-propionic orcein (Dyer, 1963). Permanent microscope slides were prepared using Euparal. Chromosome numbers were based on the counts from an average of 20 cells from five different individuals of each species. A conventional microscope was used to analyze the mitotic preparations and the photographs were taken with a Zeiss Axioplan microscope equipped with a Canon Power Shot A640 camera.

2.3. Geographic distribution of cytotypes

For the map-based presentation of the data, 144 populations of *Lessingianthus* species have been considered, including chromosome counts (28 counts) carried out here together with previous published counts (116 previous counts). The identity of the species was corroborated and the geographical coordinates or detailed descriptions of the collection sites were taken into account. Thus, chromosome counts of *L. bardanoides* (Jones, 1979; Turner et al., 1979), *L. glabratus*, *L. linearis*, *L. pumillus*, *L. rubricaulis* (Jones, 1979), *L. lorentzii* (Galiano and Hunziker, 1987), *L. rugulosus* (Dematteis, 2002) and *L. sellowii* (Dematteis, 1997, 1998) were not considered for the cytogeographic analysis and ENM, since these specimens have a different basic chromosome number from that typical of the genus ($x = 16$). However, the contribution of these authors was considered and the chromosome counts are listed in the table of previously published data (Supplementary Table S1).

Maps were made using the QGis 3.4.2-Madeira software (QGIS Development Team, 2018), which were recorded for ecoregions and biomes of South America sensu Olson et al. (2001). For this, the geographic coordinates of each sampling site of the populations analyzed in this study were recorded by GPS. In addition, the coordinates of other populations published in previous studies were incorporated (Supplementary Table S1). In cases that were not georeferenced, the coordinates of the municipalities were recorded following the guidelines and tools for georeferencing (Guide to Best Practices for Georeferencing available at https://www.gbif.org/) proposed by Chapman and Wieczorek (2020).

2.4. Ecological niche modeling (ENM) and niche overlap

To estimate the niche difference between diploids and polyploids, we used a geographical approach (ENM) and an environmental approach (PCA).

The abiotic environmental associations (climatic and edaphic) of diploids and polyploids ($4x$, $6x$, $8x$, $10x$ and $11x$) were evaluated using ecological niche modeling (ENM) with the maximum entropy algorithm implemented in MaxEnt ver. 3.4.1 software (Phillips et al., 2006). Although polyploids represent lineages with multiple origins, we followed the same grouping of cytotypes proposed in the genera *Solanum* L. (Hijmans et al., 2007) and *Fosterella* L.B. Sm. (Paule et al., 2017). The *Lessingianthus* locality records were obtained from the collections of the working group and from previous studies that reported ploidy levels (Supplementary Table S1). The records were compiled and checked rigorously for duplicate data. To avoid a spatial autocorrelation bias, the occurrence points were filtered, keeping only one every 5 km. Thus, 46 geo-referenced points corresponding to the diploids and 98 geo-referenced points corresponding to the polyploids were used for the analysis. Climate data were downloaded from the CHELSA database (Karger et al., 2017) with a resolution of 2.5′. Edaphic data were obtained from ISRIC-World Soil Information database (Hengl et al., 2017) (Supplementary Table S2). For the edaphic data we calculated a weighted mean from five depths (0–5, 5–15, 15–30, 30– 60, 60–100 cm) to generate a single value for the first meter of soil for each layer, and then we resampled the data to 2.5″ resolution to match the CHELSA dataset, using QGis 3.4.2-Madeira (QGIS Development Team, 2018).

Correlations between all the variables were evaluated by Pearson's pairwise correlation analysis ($r > 0.8$). The CONABIO's Niche ToolBox platform was used for this analysis (Osorio-Olvera et al., 2018). Following this analysis, 18 environmental (eight climatic and ten edaphic) variables were selected (Supplementary Table S2). To assess the preferences of ploidy levels (diploid vs. polyploid) for these selected climatic and edaphic variables, the non-parametric Wilcoxon rank-sum test (= Mann-Whitney U-test) was performed, as the variables did not fulfil the normality assumption (Shapiro- Wilk test). The data were visualized using box plots.

In addition, a principal component analysis (PCA) with these climatic and edaphic variables were performed. All statistical analyses were performed in R 4.0.2 software (R Core Team, 2020) with the package "FactoMineR" v. 2.4 (Lê et al., 2008) and additional tools from the "factoextra" v. 1.0.7 package (Kassambara and Mundt, 2020).

The ENMs were made considering diploids and polyploids. The parameters used to run MaxEnt were calibrated through the R-based Wallace platform (Kass et al., 2018). The three best models were selected based on the lowest values of the corrected Akaike information criterion (AICc) and the number of parameters. The final ENM was performed when the optimal parameters of the different models were defined. For the diploids, MaxEnt was run using the following settings replicates= 10; hinge features; maximum number of iterations= 500; regularization multiplier= 2; logistic output format and maximum number of background points = 10,000. For the polyploids: replicates= 10; linear, quadratic, hinge features; maximum number of iterations= 500; regularization multiplier= 3; logistic output format and maximum number of background points= 10,000. To evaluate the model performance statistically, the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Phillips et al., 2006) was used. The AUC is a threshold-independent measure of model performance and varies from 0 to 1; 0.5 means no predictive ability or randomness and 1.0 shows perfect predictive ability (Fielding and Bell, 1997). The final models were converted into a binary format to calculate the suitable habitat of each cytotype and assess the niche overlap between diploids and polyploids. To generate these binary maps, the minimum predicted suitability value for an occurrence location used to build the model was used as the threshold values.

The niche overlap was tested with ENMTools v 1.4.4 (Warren et al., 2010) to examine the niche divergence between diploids and polyploids. Schoener's D (Warren et al., 2008) and Hellinger's-based I (Schoener, 1968) indexes were calculated based on the habitat suitability comparison from ENM. Both indexes range from 0 (complete divergence/ no overlap) to 1 (high similarity/complete overlap, niche being equally suitable for both species) (Warren et al., 2008; Broennimann et al., 2012). Then, the identity test was performed to validate whether the niche-overlap scores obtained exhibited statistically significant values (Warren et al., 2008). A pseudo replicated null distribution was generated with this test with 100 replicates. Finally, Schoener's D and Hellinger's I were compared with the generated null distribution. The null hypothesis of this test (the observed values of niche overlap do not differ from random values) is rejected when the estimated value for D and/or I is significantly different from the null distribution.

3. Results

3.1. Chromosome counts

In this study, mitotic chromosome numbers are reported for 28 populations of 16 species of *Lessingianthus*. A list of all samples studied, their geographic origin, and herbarium voucher information are provided in Table 1.

Four species were analyzed for the first time (marked with ''*'' in Table 1), three hexaploids with $2n = 96$ (*L. parvifolius*, *L. vepretorum* and *L.*"bolivianensis" sp. ined., Fig. 1D,H,I) and one decaploid taxon with $2n = 160$ (*L. roseus*, Fig. 1E). A new hexaploid cytotype with $2n = 96$ (marked with ''†'' in Table 1) was also found in *L. lanatus* in a population from Pedro Juan Caballero (Department of Amambay, Paraguay) (Fig. 1B). In addition, counts of new localities (marked with "◊" see Table 1) from Corrientes and Chaco provinces in Argentina are also reported for *L. glabratus* (Fig. 1A), *L. niederlinii* (Fig. 1C) and *L. rubricaulis* (Fig. 1F,G). The chromosome numbers observed in the remaining taxa are in agreement with previous studies.

All 144 populations studied cytogeographically had basic chromosome number $x = 16$. The chromosome numbers ranged from $2n = 32$–$2n = 176$ and the cytotypes observed were $2x$, $4x$, $6x$, $8x$, $10x$ and $11x$. Almost all the species showed one ploidy level (Supplementary Table S3) with the exception of four taxa: *L. laniferus*, *L. rubricaulis* and *L. sellowii*, which had diploid and tetraploid cytotypes, whereas *L. lanatus* had a diploid and a new hexaploid cytotype. Among the cytotype diversity observed in cytogeographically analyzed populations, tetraploid was the most frequent ploidy level (38.88%), followed by the diploids (32.63%), hexaploids (12.5%), octoploids (10.41%), decaploids (4.16%) and finally by undecaploids (1.38%) (Table 2).

3.2. Geographic distribution of cytotypes

The geographic distribution of the cytotypes is apparently random, occurring in 17 South American ecoregions (Fig. 2A). Among the cytotypes, the diploids have the largest distribution area, occupying 13 ecoregions (see map), whereas the tetraploids and hexaploids occur in twelve and seven regions, respectively (Fig. 2D and see Supplementary Table S4). The remaining cytotypes have more restricted distributions. Most of the octoploid populations occur in the southwest of the Alto Paraná Atlantic forest in Paraguay, and only some populations are found in the southwest of the Cerrado, Chiquitano dry forest of Brazil and the Humid Chaco of Argentina. Decaploid populations are mainly distributed in the southwest of the Alto Paraná Atlantic forest in Argentina, with one population in the west of the Bolivian Yungas (Bolivia) and one population in the southeast of the Cerrado (Brazil). The chromosome number $11x$ represents the rarest cytotype and was found in specific locations in the Uruguayan savanna (Uruguay).

The Alto Paraná Atlantic forest and Cerrado exhibit the highest diversity in ploidy levels (Fig. 2D; and see Supplementary Table S4); almost all cytotypes were found with the only exception of $11x$. The high distribution of these cytotypes is consistent with the transition zone between these two ecoregions in northeastern Paraguay (Dept. Amambay) (Fig. 2B) exhibiting numerous $2x$, $4x$, $6x$ and $8x$ populations. Many of these populations have overlapping distributions and can be found co-occurring in the same geographic area, such as in the case of six species,

Table 1

Mitotic chromosome numbers, ploidy level, locality details, and voucher information of 28 populations of *Lessingianthus* species analyzed in this study. First count for the taxon are indicates with ''* '', new cytotype with ''†'' and counts for new localities with “◊”.

Species	2*n*	Plody level	Locality, Voucher specimen	Lat. S	Long. W	
L. brevifloius (Less.) H.Rob.	32	2*x*	Argentina. Misiones. Dept. San Ignacio. 4 Km S of San Ignacio, road to Teyú Cuaré Park. Dematteis. 2749 (CTES).	-27.27	-55.56	
	32	2*x*	Argentina. Corrientes. Dept. Saladas. Margen of Ayo. San Lorenzo. M. Dematteis et al., 2767 (CTES).	-28.11	-58.77	
	32	2*x*	Argentina. Corrientes. Dept. Capital, Riachuelo. Angulo. 76 (CTES).	-27.56	-58.74	
	32	2*x*	Argentina. Misiones. Dept. San Ignacio. Sandy fields to 3 km de Parque Teyú Cuaré . Dematteis et al., 3050 (CTES).	-27.56	-55.55	
L. cataractarum (Hieron.) H.Rob.	64	4*x*	Argentina. Misiones. Dept. San Pedro. National Park Moconá. Dematteis et al., 3097 (CTES, MBM, G, SI).	-26.27	-53.70	
	64	4*x*	Argentina. Misiones, Dept. San Pedro, Moconá National Park. Vega et al., 33 (CTES).	-27.15	-53.89	
L. centauropsideus (Hieron.) Dematt.	96	6*x*	Argentina. Salta. Dept. Santa Victoria 0.3.8 km S of Los Toldos, on the road to Lipeo. Dematteis et al., 2936 (CTES).	-22.31	-64.7	
	96	6*x*	Argentina. Salta. Dept. Santa Victoria. Quebrada Honda, 10 km S of Los Toldos, on the road to Lipeo. Dematteis et al., 2939 (CTES)	-22.34	-64.72	
L. glabratus (Less.) H.Rob.	128	8*x*	Argentina. Corrientes, Dept. Santo Tomé , 13 km N of Galarza, provincial route 41. Ea. La Palma. Dematteis et al., 4272 (CTES)	-28.01	-56.58	◊
L. lanatus (Cabrera) Dematt.	96	6*x*	Paraguay. Dept. Amambay, P. J. Caballero. Dematteis and Vega, 4290 (CTES).	-22.58	-55.72	†
L. niederleinii (Hieron.) H.Rob.	96	6*x*	Argentina Misiones. Dept. General Manuel Belgrano. Campina de Américo. Angulo, 82 (CTES).	-26.3	-53.69	
	96	6*x*	Argentina. Corrientes. Dept. Santo Tomé , 40 km W de Virasoro, road to garruchos. Dematteis et al., 4279 (CTES).	-27.99	-55.82	◊
	96	6*x*	Paraguay. Dep. Canindeyú. Lagunita, 3 km N of route 10, road to Monte Sinaí . Dematteis et al., 2870 (CTES).	-24.49	-55.81	
L. parvifolius (Chodat) H.Rob.	96	6*x*	Paraguay. Dept. Amambay, P. J. Caballero. Dematteis and Vega, 4291 (CTES).	-22.58	-55.72	*
L. polyphyllus (Sch. Bip. ex Baker) H. Rob.	64	4*x*	Argentina. Misiones. Dept. San Ignacio, 4 km S of San Ignacio, house of Horacio Quiroga. Angulo, 83 (CTES).	-27.26	-55.55	
L. pseudoincanus (Hieron.) Dematteis & Angulo	64	4*x*	Argentina. Corrientes. Dept. Capital, Barrio Molina Punta. Angulo, 76 (CTES).	-27.46	-56.77	
	64	4*x*	Argentina. Corrientes. Dept. Capital, Barrio Molina Punta. Angulo, 78 (CTES).	-27.46	-56.7	
	64	4*x*	Argentina. Chaco. Dept 1° de Mayo. Colonia Benítez. Angulo, 81 (CTES).	-27.41	-58.78	
L. pusillus (Dematt.) M.B. Angulo,	32	2*x*	Argentina. Corrientes. Dept. Capital, Perichón, 3 km of river. Angulo, 79 (CTES)	-27.42	-58.75	

(*continued on next page*)

Table 1 (*continued*)

Species	2 *n*	Plody level	Locality, Voucher specimen	Lat. S	Long. W	
L. roseus (Mart. ex DC.) H.Rob.	160	10*x*	Brazil, Minas Gerais, Mun. Santana do Riacho, Serra do Cipó National Park, Marques and Contro, 544 (HUFU).	-19.34	-43.62	*
L. rubricaulis (Humb. & Bonpl.) H.Rob.	32	2*x*	Argentina. Misiones. Dept. Obera. Campo Viera, Dematteis et al., 4278 (CTES).	-27.38	-55.11	
	32	2*x*	Argentina. Chaco. Dept. 1° de Mayo. Colonia Benítez. Angulo, 80 (CTES).	-27.33	-58.95	◊
L. sellowii (Less.) H. Rob.	64	4*x*	Argentina. Misiones. Dept. Candelaria: road to Profundidad, 5 Km of route 12. Angulo, 85 (CTES).	-27.41	-55.61	
L. teyucuarensis (Cabrera) Dematt.	160	10*x*	Argentina. Misiones. Dept San Ignacio. 3 km of Teyú Cuaré Provincial Park. Dematteis et al., 3049 (CTES).	-27.27	-55.55	
	160	10*x*	Argentina. Misiones. Dept. San Ignacio. 3 km of Teyú Cuaré Provincial Park. Angulo, 110 (CTES).	-27.27	-55.55	
L. vepretorum (Mart. ex DC.) H. Rob.	96	6*x*	Brazil. Minas Gerais. Mun. Diamantina. State Park of Biribiri. Marques and Contro, 553 (HUFU).	-18.12	-43.58	*
	96	6*x*	Brazil. Minas Gerais. Mun. Diamantina. State Park of Biribiri. Marques and Contro, 554 (HUFU).	-18.14	-43.61	*
Lessingianthus "bolivianensis" sp. ined.	96	6*x*	Bolivia. Dept. Santa Cruz, Chiquitos Province. Natural Reserve of Tuca Vaca Valley. Dematteis et al., 3929 (CTES).	-18.32	-59.58	*

each with a different cytotype, coexisting in the locality of Pedro Juan Caballero in Amambay (Paraguay).

On the other hand, another transition zone with a high diversity of cytotypes was observed in northeastern Argentina (Fig. 2 C). This transition zone, occurring in the zone between the Alto Paraná Atlantic forest and the Southern Cone Mesopotamian savanna in northeastern Argentina (Fig. 2 C), also showed a high cytotype diversity with 2*x*, 4*x*, 6*x*, and 10*x* populations from eight species.

3.3. *Ecological niche modeling (ENM) and niche overlap*

The validation metrics (AUC), threshold values and the contribution of variables for diploid and polyploid ENMs are detailed in Table 3. The AUC values indicate that the models performed well at predicting distributions.

The ENM predict suitable localities for diploids and polyploids that mostly match their known distributions. However, the models predict larger suitable areas in regions where there are no known occurrence localities for the genus. The ENMs reveal a high predicted suitability (greater than 0.75) for diploids in southern Brazil, central and northeastern Argentina, most of Uruguay, eastern Paraguay and Bolivia, and a strip bordering the Andean Cordillera from Bolivia to Ecuador (Fig. 3 A). For polyploids the area of suitability is similar to that of diploids in extension, however the areas of high suitability (greater than 0.75) are more restricted, being concentrated in southern Brazil, eastern Paraguay, northwestern Argentina and small isolated areas in central and northern Argentina and southern Bolivia (Fig. 3B).

The variables that most contributed to both diploid and polyploid ENMs were the Bio 18 (Table 3). For diploids, the next most important contributing variables were Bio 2, Bio 1, Bio 3, ferrasol soils, Bio 12 and pH (between 17.9% and 5.8%). For polyploids, they were Bio 3, Bio 2, Ph, Bio 1, and Bio 14 (between 20.2% and 6.1%). The remaining variables contributed $< 3\%$ to the construction of the models.

The results of the non-parametric Wilcoxon rank-sum test for each of the variables (used in the ENM) between diploids and polyploids revealed no significant differences (with the exception of Bio 3, 13, 14 and phosphorus content), pointing to a lack of ecological differentiation between the two ploidy groups (Supplementary Fig. S1).

Additionally, the climatic niches of diploids and polyploids were compared with a PCA on the full set of 18 environmental variables used for the ENMs (Fig. 3 C). The results of PCA showed that the first two components accounted for 53.1% of the total variance. The directionality of the loadings for components 1 and 2 was quite variable and both axes are related with climatic and edaphic variables. Cation Exchange Capacity (CECSOL) and available water capacity content (WWP) of the soils contributed most to component 1, followed by contributions from bulk density (BLDFIE), carbon (ORCDRC) and iron content of soils (ferrasol soils) (Supplementary Fig. S2A). Whereas annual precipitation (Bio 12), followed by contributions from clay (CLYPPT) content and pH of soils are the variables that contributed most to component 2, as well as the precipitation in warm (Bio 18) and wet (Bio 13) periods (Supplementary Fig. S2B). The PCA shows that considering the first two components, the diploid and polyploid niches overlap, and the polyploids fall almost completely within the diploid niche. Furthermore, it can be seen that the diploid niche is larger (greater environmental amplitude) than that of the polyploids.

The diploids and polyploids showed high values of niche overlap within the environmental space, with a value of $D = 0.75$ and $I = 0.94$ (Fig. 3D), suggesting a high level of niche conservatism between both groups.

4. Discussion

4.1. *Chromosome counts*

The present study summarizes all the known data on the chromosome numbers of the *Lessingianthus* species. Among the species analyzed here, different ploidy levels (2*x*, 4*x*, 6*x*, 8*x* and 10*x*) were found, and the chromosome numbers for four taxa (*L. parvifolius*, *L. roseus*, *L. vepretorum* and *L.*"bolivianensis" sp. ined.) are reported for the first time, as well as

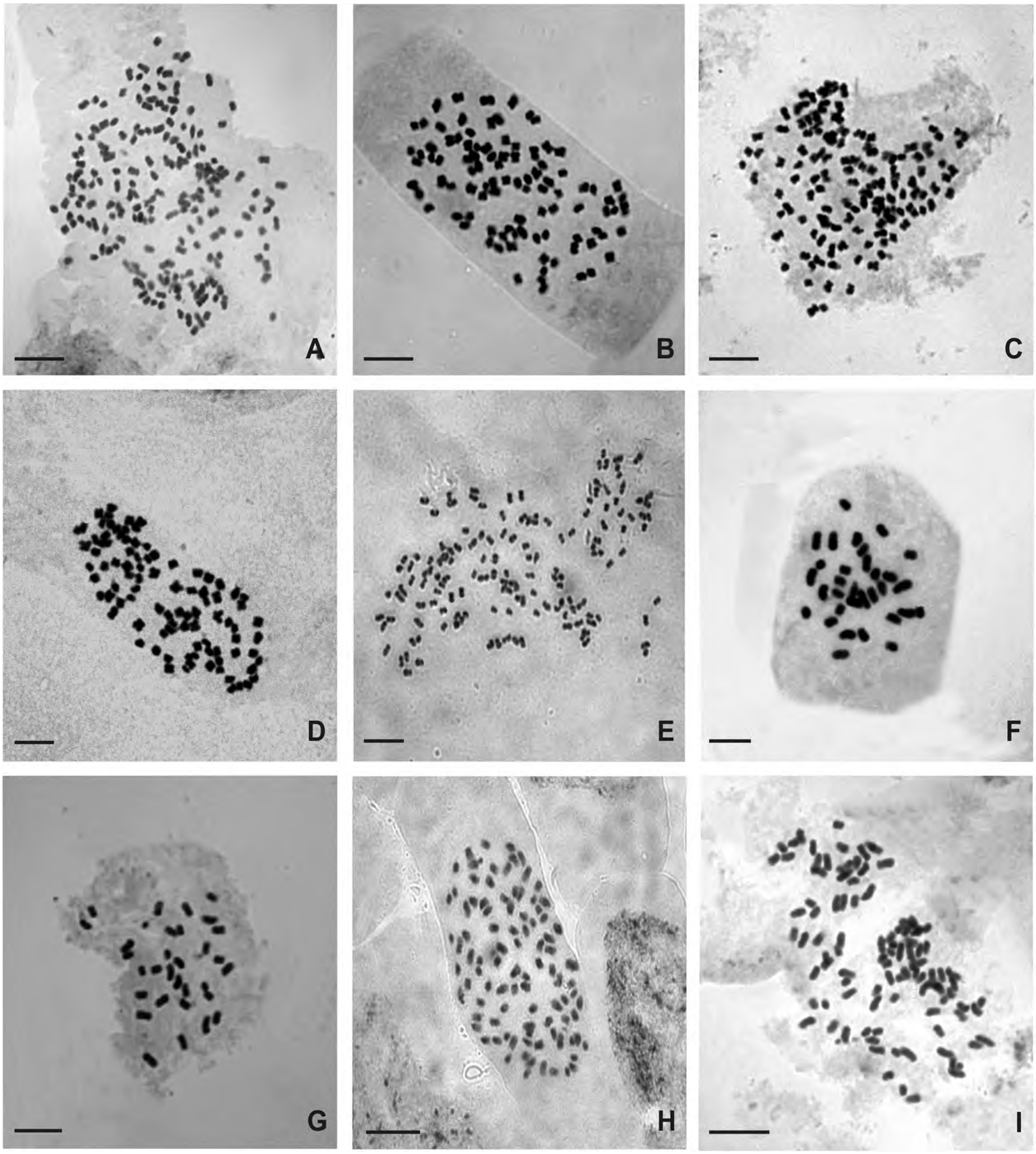

Fig. 1. Somatic chromosomes of *Lessingianthus*. A, *Lessingianthus glabratus* (2 *n* = 8*x* = 128); B, *Lessingianthus lanatus* (2 *n* = 6*x* = 96); C, *Lessingianthus niederleinii* (2 *n* = 6*x* = 96); D, *Lessingianthus parvifolius* (2 *n* = 6*x* = 96); E, *Lessingianthus roseus* (2 *n* = 10*x* = 160); F-G, *Lessingianthus rubricaulis* (2 *n* = 2*x* = 32); H, *Lessingianthus vepretorum* (2 *n* = 6*x* = 96); I, *Lessingianthus* "bolivianensis" (sp. ined.) (2 *n* = 6*x* = 96). Scale bar: 5 μm.

Table 2
Cytotype diversity found within 144 sampled populations of Lessingianthus. Percentages are always calculated relative to the total number of sampled populations.

Ploidy levels	Number of populations	Frequency
2*x*	47	32.63%
4*x*	56	38.88%
6*x*	18	12.5%
8*x*	15	10.41%
10*x*	6	4.16%
11*x*	2	1.38%

a new cytotype for one species (*L. lanatus*) and counts for populations of new geographical localities (*L. glabratus*, *L. niederleinii* and *L. rubricaulis* from Argentina). Therefore, with the results of this study presented in the form of a review, the cytogenetic complexity previously suggested for the genus (Angulo and Dematteis, 2012a) is confirmed.

The chromosome count found in *L. glabratus* (2 *n* = 128) disagrees with previous counts carried out by Jones (1979) who recorded *n* = 17, ca. 17 +Bs, 51 (51II), 51 (48II+6I), 52, ca. 67 or 68 for the Brazilian populations of this species. This disparity in chromosome numbers may be attributed to incorrect counts (due to the small size of the chromosomes) or to the misidentification of the species (mainly in taxonomically complex groups) (Guerra, 1988). The taxonomic complexity of certain plant groups can create serious problems in specimen identification due to their diversity and/or the existence of hybrids and polyploids that create individuals or species with intermediate

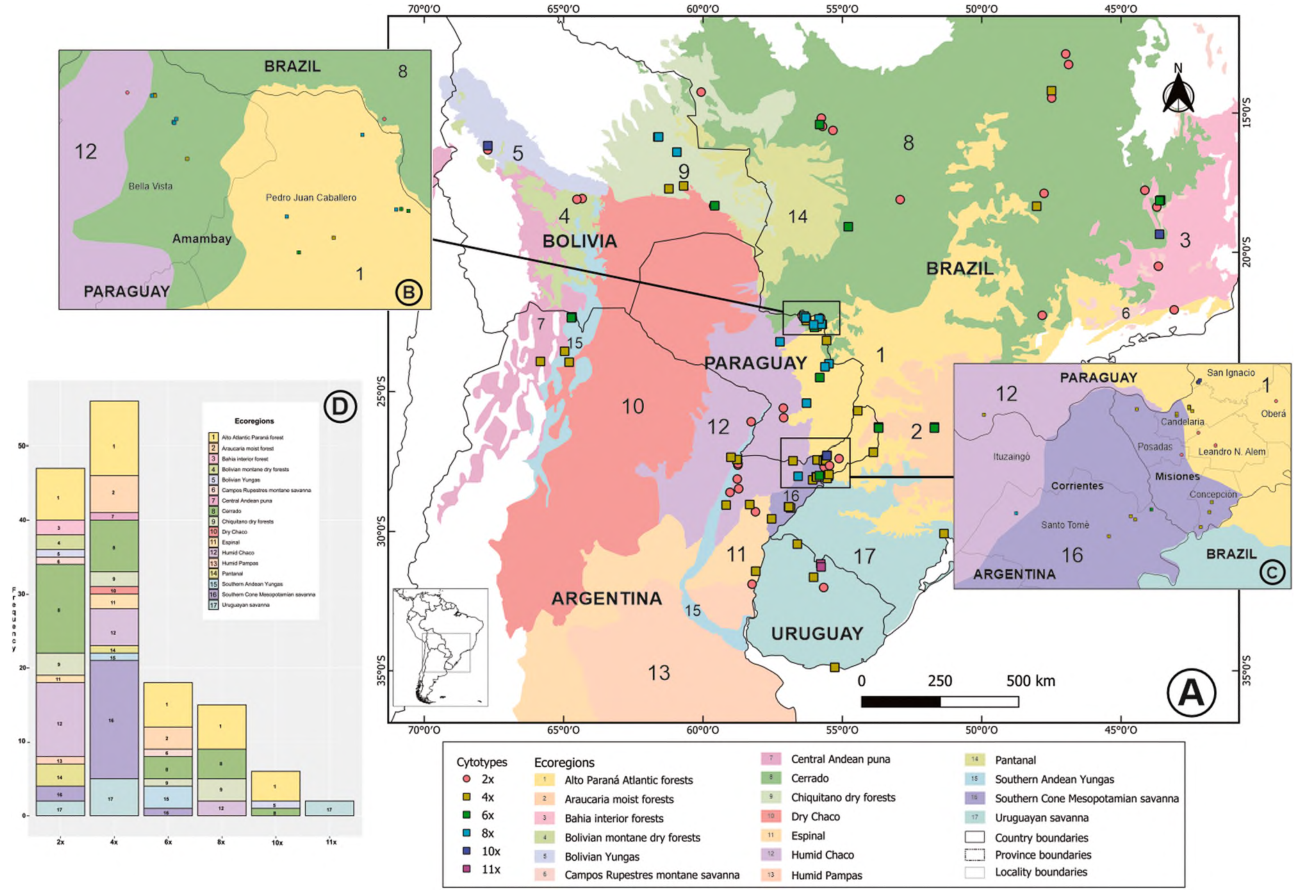

Fig. 2. Map showing the geographical distribution of cytotypes of *Lessingianthus* throughout South America. A, General view of the study area. The line indicates the limit of the ecoregions according to Olson et al. (2001); B, Area show populations in a transition zone between Cerrado and Alto Paraná Atlantic Forest in northeastern Paraguay; C, Area show populations in a transition zone between Alto Paraná Atlantic Forest and Southern Cone Mesopotamian savanna in northeastern Argentina; D, Distribution of cytotypes of *Lessingianthus* in relation to ecoregions (according to Olson et al., 2001).

Table 3
Validation metrics (AUC), threshold values used for binary maps, and variables contribution for diploid and polyploid ENMs. For variable codes see Supplementary Table S2.

	Diploids	Polyploids
AUC	0.887	0.924
Threshold	0.287	0.091
Variables	**Percent contribution**	
Bio 18	31.9	29.4
Bio 2	17.9	15.1
Bio 1	17.2	7.2
Bio 3	8.9	20.2
Ferrasol soils	8	2.4
Bio 12	6.4	1.1
pH	5.8	13.2
CLYPPT	1.9	0.6
CECSOL	0.7	1.2
CRFVOL	0.6	0.3
Bio 10	0.4	0.8
NITROGEN	0.4	0
WWP	0	1.5
PHOSPHORUS	0	0.4
ORCDRC	0	0
Bio 13	0	0.4
Bio 14	0	6.1
BLDFIE	0	0

morphological characters (Stace, 1989). Any of these could be the causes for the mismatching of chromosome counts in some species in this study.

The chromosome counts carried out here together with the previous counts (Angulo, 2012; Angulo and Dematteis, 2009a; b, 2012a, 2012b, 2015, 2016; Dematteis, 1998, 2002; Dematteis and Fernández, 2000; Dematteis et al., 2007; Oliveira et al., 2012), agree that $x = 16$ is the basic chromosome number of the group. Although all the species examined in the present study present $x = 16$, some previous studies have reported other base chromosome numbers for some species, such as *L. lorentzii*, (Hieron.) H.Rob. (Galiano and Hunziker, 1987), *L. pumillus* (Vell.) H.Rob. (Jones, 1979) and *L. rugulosus* (Sch.Bip. ex Baker) H.Rob. (Dematteis, 2002). However, these taxa have all the diagnostic features of *Lessingianthus*, including the distinctive "type B'' pollen (Angulo and Dematteis, 2010), so further cytological studies should be carried out on these species to confirm their chromosome numbers, as has been done in other species of the group (*L. bardanoides*, *L. glabratus*, *L. linearis*, *L. niederleinii*, *L. rubricaulis*, see Supplementary Table S1).

The first chromosome counts were reported for *L. parvifolius*, *L. roseus*, *L. vepretorum*, and *L.*"bolivianensis" sp. ined. The latter species is hexaploid with $2n = 96$, which appears to be closely related to the octoploid *L. scabrifoliatus* (Hieron) H.Rob. with $2n = 128$. In addition to the chromosome number, these species can also be distinguished by their morphology, such as leaf apices, head size and cypsela indumentum. Therefore, the combination of cytogenetical and morphological features support the treatment of both taxa as different species (Dematteis and Angulo, in preparation).

In addition, a new hexaploid cytotype ($2n = 96$) was reported for a population of *L. lanatus* from northeastern Paraguay at Pedro Juan Caballero (Amambay). A prior analysis of this species reported a diploid cytotype ($2n = 32$) but for a population from the south of Paraguay (Dept. of Paraguarí) (Angulo and Dematteis, 2012a). We consider that

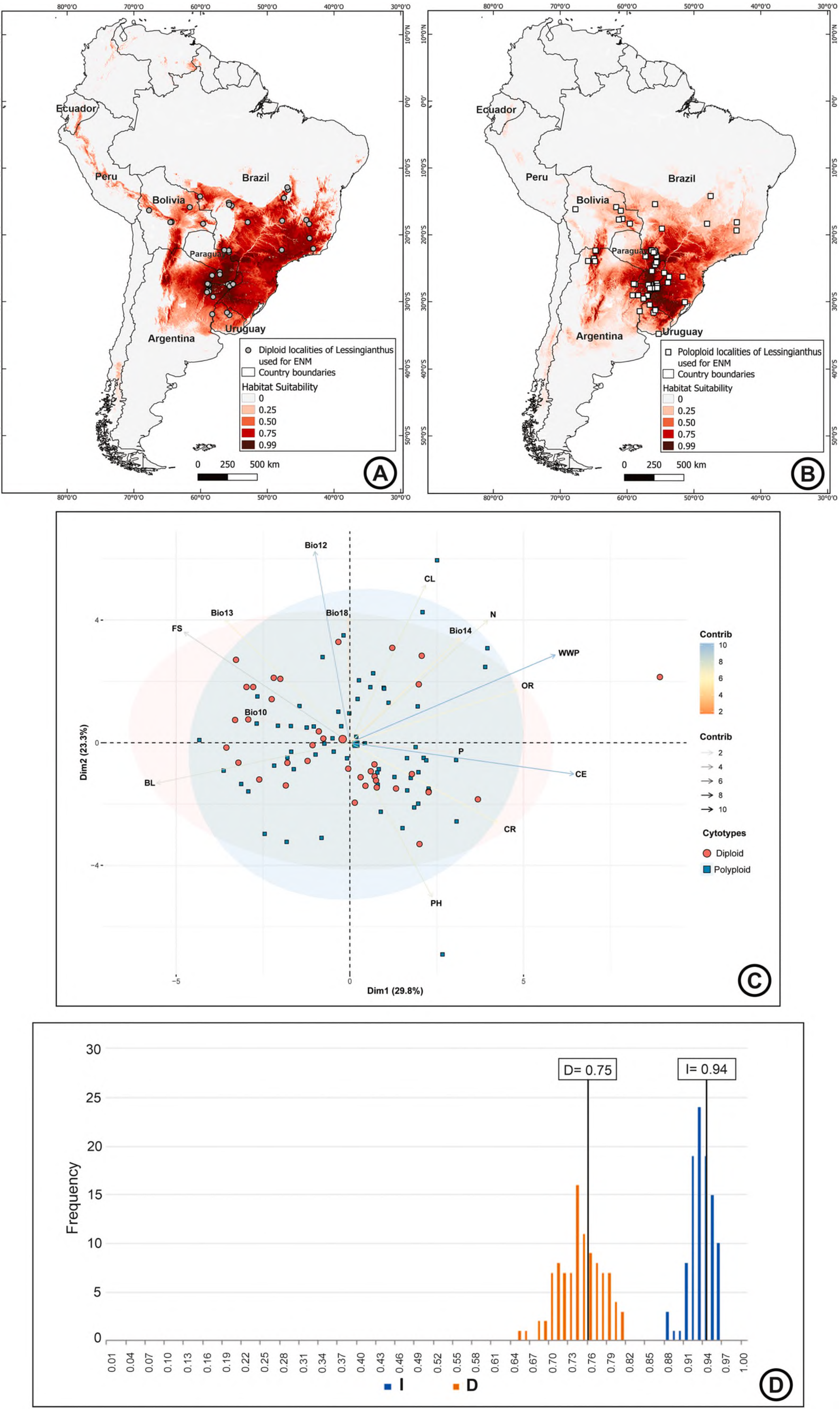

Fig. 3. Maps of the ecological niche models generated with Maxent for each cytotype: A, diploids and B, polyploids of *Lessingianthus*; C, PCA ordination plot of diploid (red circles) and polyploid (blue squares) cytotypes of *Lessingianthus* in the plane of the first two principal component axes based on the selected bioclimatic and soil data. Bio 10 = temperatures of the warmest quarter; Bio 12 = annual precipitation; Bio 13 = precipitation of the wettest month; Bio 14 = precipitation of the driest month; Bio 18 = precipitation of warmest quarter; BL= bulk density; CE= cation exchange capacity; CL= clay particles; CR= coarse fragments; Dim= dimension; FS= probability of ferrasol soils; N = total nitrogen; OR= organic carbon content; P = phosphorus content; PH= soil pH; WWP= available soil water capacity; D, Niche overlap evaluated by the identity test. D= Schoener's D index and I= Hellinger's-based I index.

both cytotypes (2*x* and 6*x*) belong to the same species (*L. lanatus*) because they share morphological features that are distinctive for this taxon (disposition of leaves on the stem, leaf shape and head size). It is essential to highlight that, according to the Flora of Paraguay, this species was only previously known from southern Paraguay (Depts. of Cordillera, Guairá and Paraguarí) (Cabrera and Dematteis, 2009), therefore a new record for this taxon for northeastern Paraguay (Dept. of Amambay) is presented here for the first time. In addition to *L. lanatus*, other species (*L. laniferus*, *L. rubricaulis* and *L. sellowii*) with ploidy variation (2*x* and 4*x*) at the intraspecific level were also observed in the genus (Angulo and Dematteis, 2009b, 2012a).

Lessingianthus rubricaulis and *L. laniferus* together with *L. pusillus* and *L. pseudoincanus* grouped in a polyploid complex named the "*L. rubricaulis* complex" (Dematteis, 2004). These species are very similar morphologically but they are distinguished by their habit, underground system, indumentum type, and the size and shape of the leaves (Dematteis, 2004). Results of the present survey add several chromosome counts for *L. pusillus*, *L. pseudoincanus* and *L. rubricaulis* and together with previous studies (Angulo and Dematteis, 2009a, 2012a, 2012b, 2015; Dematteis, 2002, 2004), show that these taxa are 2*x* (*L. pusillus*), 4*x* (*L. pseudoincanus*) or 2*x* and 4*x* (*L. laniferus* and *L. rubricaulis*). Polyploid complexes are very frequent in nature and have been the subject of much research into the mechanisms involves in their evolutionary dynamics (origin, establishment and persistence of polyploids) and in the ecological differentiation of polyploids (Afonso et al., 2021; Flatscher et al., 2015; Morales et al., 2020; Stuessy et al., 2004; Tomasello and Oberprieler, 2017). Many of these complexes have been attributed an autopolyploid origin through sexual polyploidization that involve gametic ''non-reduction'' (Lazaroff et al., 2016; Solís Neffa et al., 2022).

Sexual polyploidization is considered the most common mechanism of origin and evolution of polyploids in flowering plant species through fertilizations involving unreduced gametes, i.e. gametes that, as a result of modified gametogenesis, have the same number as the somatic chromosomes (Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998). In particular, it has been suggested that autotetraploids are formed through a pathway involving the union of two unreduced gametes produced by diploids, resulting in the production of tetraploids in a single step (bilateral polyploidization). Alternatively, tetraploids can arise in two steps (unilateral polyploidization), from the pairing of triploids resulting from the union between a reduced and a non-reduced gamete produced by diploids (Ramsey and Schemske, 1998). It is likely that this mechanism is responsible for the origin of species with different ploidy levels both in the "*L. rubricaulis* complex" and in other species of the genus with more than one cytotype.

Among the Vernonieae, *Lessingianthus* is the genus with the highest ploidy levels, the most extreme case being *L. macrocephalus* with $2n = 11x = 176$ (Angulo and Dematteis, 2012a). This species grows in southern Brazil and northeastern Uruguay (Bayón and Dematties, 2008) and so far, only two populations from Uruguay (Dept. of Rivera) have been counted (Angulo and Dematteis, 2012a). The high ploidy levels combined with odd chromosomal complements suggest irregular meiotic behavior and possible sterility of individuals.

Apomictic reproduction is very common in plants with these characteristics and it is a natural process that result in clonal reproduction by means of seeds, avoiding meiosis and fertilization, which creates offspring genetically identical to the maternal plant (Nogler, 1984). Recent reviews document the high frequency of apomictic species in 27 genera of the Asteraceae family (Hojsgaard et al., 2014, Pegoraro et al., 2020). Therefore, the occurrence of the very high and odd ploidy levels observed in *L. macrocephalus* might suggest that this species would also have apomictic reproduction. Polyploidy and apomixis can co-occur, since they share common developmental pathways. Both phenomena can be induced after a hybridization event and involve the production of unreduced gametes, restoring fertility after hybridization (Husband et al., 2013). Therefore, two possible scenarios could be explain the origin of *L. macrocephalus:* 1) a hybrid from an inter-cytotypic cross with reduced gametes from both 10*x* and 12*x* (unsampled), or 2) a hybrid between a reduced gamete from 10*x* with a non-reduced gamete from 6*x*. This hybrid (whatever its origin) could have been ephemeral in nature or could have stabilized in populations through reproduction by apomixis. Although there are no studies on hybridization in *Lessingianthus*, it is known that hybridization is possible in the tribe Vernonieae (Jones, 1977). Therefore, hybridization could not be ruled out as another reproductive mechanism within the genus.

4.2. *Geographic distribution of cytotypes*

Polyploidy is an important genetic determinant of a species geographic range (Husband et al., 2013). Botanists usually consider that (1) polyploid ranges will differ from those of the diploids, and (2) polyploid species will have wider geographic ranges (Husband et al., 2013). Our results, however, are not consistent with these assumptions. Both diploids and polyploids occupy the same geographic ranges and they have wide ranges of distribution. Diploid populations showed the largest range, occurring in 13 neotropical ecoregions (see map). Many of these ecoregions were also occupied by other cytotypes, and therefore, populations with different ploidy levels can be found co-occurring in the same area. Only four diploid populations occur exclusively in a particular ecoregion without any polyploids. Such is the case of *L. coriarius* and *L. membranifolius*, which are only found in the Bolivian montane dry forest (Bolivia), whereas one 2*x* population of *L. rubicaulis* inhabits the interior forests of Bahia (Brazil) and two populations of *L. brevifolius* in the Humid Pampas (Argentina). However, the latter two species have a wide distribution and were also found in other ecoregions. Thus, we can establish that the diploid cytotypes of the genus occupy large distribution areas and, in many cases, may occupy the same distribution ranges as the polyploid populations.

Our results showed that the Alto Paraná Atlantic forest and Cerrado were the ecoregions with the highest diversity of ploidy levels. These neotropical ecoregions have been recognized as biodiversity hotspots due to the remarkable species richness and endemism of several groups of organisms (Ceballos and Ortega-Baes, 2011; Mohebalian et al., 2022; Myers et al., 2000), which may be caused by environmental heterogeneity, together with polyploidization and hybridization as suggested in several studies (Echternacht et al., 2011; Schley et al., 2022). Our geographic analyses revealed two transition zones with a high diversity of ploidy levels and species. One between the Alto Paraná Atlantic forest and the Cerrado on in the border between the southeast of Brazil and northeastern Paraguay, and another between the Alto Paraná Atlantic forest and the Southern Cone Mesopotamian Savanna (neotropical ecoregions that encompass extensive natural grassland and savanna communities, Bilenca and Miñarro, 2004) in northeastern Argentina.

In both transition zones, most of the populations with different ploidy levels belonging to related species were found co-occurring in the same area (Pedro Juan Caballero in Amambay, Paraguay and the border between Corrientes and Misiones, Argentina). Both zones were recognized as extremely rich in terms of their flora (Zuloaga et al., 2008, Zanotti et al., 2020). Via do Pico et al. (2019), also found a high diversity of cytotypes and species in the Pedro Juan Caballero area (Amambay, Paraguay), but for the genus *Chrysolaena* (Vernonieae, Asteraceae). These authors suggested that hybridization and polyploidization events occurred in this geographically small area, which would have given rise to certain hybrid species such as *C. cristobaliana* Dematt. (a heptaploid taxon and its probable parents could be *C. cognata* (Less.) Dematt., 8*x* and *C. platensis* (Spreng.) H. Rob., 6*x*). There is no doubt that the cytotype diversity (2*x*, 4*x*, 6*x*, 8*x*) observed in this small area is also high for *Lessingianthus*. However, so far, no cytotypes of local origin or showing morphological differences (due to their independent origin) to the corresponding cytotypes sampled elsewhere were found to assume that hybridization events could be occurring in these areas. However, the high cytotype and species diversity in these transition zones is undeniable and further research in these areas would be of great interest.

Angulo et al. (2021) evaluated the effect of climate change on the current and future suitable habitat distribution of threatened *Lessingianthus* species from the Brazilian Cerrado showing a tendency for most climatically stable areas to be located in the transition zone between the Cerrado and the Alto Paraná Atlantic forest (limit between the southeast of Brazil and northeastern Paraguay). In the present study, we also observed that much part of the cytotype diversity in the genus was found in these transition zones. However, these regions have been subject to serious habitat deterioration mainly caused by human activities, in addition to having a low number of Protected Areas (IPBES, 2019). Therefore, the need to conserve these areas with a significant diversity of species of different ploidy levels together with the greater biotic stability observed for future scenarios becomes more evident; as they could act as important refuges that ensure the long-term persistence of biodiversity.

4.3. Ecological niche modeling (ENM) and niche overlap

Contemporary climate (i.e. temperature, precipitation and climate seasonality) and past climate change have been widely recognized as determinants of species diversity patterns (Currie, 1991; Hawkins et al., 2003; Montoya et al., 2007; Svenning and Skov, 2007). However, the species diversity–climate relationship (the correlation between species diversity pattern and climate) varies significantly across clades (e.g. animals, Buckley et al., 2010, plants, Hawkins et al., 2011), which is one of the reasons why consistent mechanisms underlying large-scale patterns of species diversity have not been found (Wang et al., 2021).

Our results reveal that there are few differences in both the geographic distribution and the environmental niche between the diploid and polyploid cytotypes of *Lessingianthus*. The assumption that polyploidization results in changes in environmental preference with the establishment of polyploids in different environmental niches than diploids is one of the hypotheses considered when addressing environmental niche modelling studies in different cytotypes (Laport et al., 2013; Manzaneda et al., 2012; Godsoe et al., 2013; Castro et al., 2019). However, this assumption is not always true and shared environmental preferences between diploids and polyploids have been observed in many taxa (Castro et al., 2019; McIntyre, 2012). Most of these ecological studies have focused on a single species with different cytotypes and few studies have studied multiple species (Glennon et al., 2014; Martin and Husband, 2009; Visser and Molofsky, 2015). Therefore, our results provide further information to deepen this assumption.

In *Lessingianthus* we can observe that niche overlap is high between diploids and polyploids, indicating similar climatic niches for both ploidy levels. If we consider that polyploid species arose from diploids, phylogenetic niche conservatism (PNC) could explain our results. PNC occurs when phylogenetically related taxa would be likely to occupy more similar environments, its occurrence suggests that some process is limiting divergence between closely related species (Losos, 2008). PNC is based on the hypothesis of the allopatric speciation model, which states that there is a general tendency among species to remain in ecologically similar areas to those occupied by the ancestral species (Peterson et al., 1999). Phylogenetically close species are more likely to inhabit environments that have some similarity, thus, to some extent, niches are being conserved (Peterson et al., 1999). However, niches cannot be conserved indefinitely, as few sister species can share identical or equivalent niches completely (Wiens and Graham, 2005; Warren et al., 2008). Somewhere along the evolutionary scale, niche evolution or innovation would have to emerge. Based on these assumptions, the *Lessingianthus* diploids and polyploids would be at a time in their evolution in which their niches have not yet diversified.

Although the phylogenetic relationships between diploids and polyploids of *Lessingianthus* have not been established, PNC justifies the comparison of polyploids with diploid congeners, even if the specific diploid parents of the polyploid species are not known. There are studies that have analyzed PNC without explicitly identifying diploid parents (Martin and Husband, 2009), and it has been reported in several taxa of the Asteraceae (Kantar et al., 2015; Suárez-Mota et al., 2015). Therefore, the high similarity between the niches of diploids and polyploids in *Lessingianthus* would indicate the presence of PNC in the group.

The PCA results based on the bioclimatic and edaphic data reinforce the niche overlap analysis, showing that the niches of diploids and polyploids are very similar. In general, diploids and polyploids grow under similar conditions in terms of annual precipitation (Bio 12, mean 1500 mm), soils with similar carbon (ORCDCR) and clay (CLYPPT) content, and bulk density (BLDFIE), showing that there are no significant ecological differences between the two ploidy groups. Although some trends were observed for polyploids to occupy areas with higher precipitation in the wet period (Bio 18) and soils with higher mineral (higher cation exchange capacity, CECSOL) content and higher values pH than diploids, the differences in these variables were not significant for either ploidy levels. Few environmental variables showed a significant relationship with the distribution of both cytotypes, such as the presence of diploids in areas with the highest precipitation in the wettest months (Bio 13) and isothermality (Bio 3), and polyploids to occupy areas with the highest precipitation in the driest months (Bio 14) and soils with high values of phosphorus content. Many authors believe that polyploidy may result in greater adaptability (Doyle et al., 2008; Te Beest et al., 2012) and could result in polyploids inhabiting more extreme environments. The idea that polyploids inhabit colder and drier habitats than their diploid relatives (Gunn et al., 2020; Te Beest et al., 2012) was partially observed among *Lessingianthus* cytotypes, as certain trends were observed in some variables related to temperature (Bio 3) and precipitation (Bio 13 and 14). However, as diploids and polyploids can co-exist in the same area, this habitat differentiation was not observed between the two ploidy levels.

Dawson et al. (2011) have proposed some general responses of species to climate change: environmental tolerance (e.g. phenotypic plasticity, changes in phenology, changes in habitat preferences or migratory timing), shifting ranges and abundance, distribution shift, and extinction. When the climatic tolerance ranges of a species are wide enough to encompass the new conditions resulting from climate change, then they could potentially adapt (Holt, 1990). Conversely, if narrow tolerance ranges and strong niche conservatism are assumed, then species would have to shift their geographic distributions in response to global warming (Wiens et al., 2010). Previous research has shown that niche conservatism could be a danger to the global biota (Wiens and Graham, 2005), as niche evolution rates have been seen to be much slower than projected climate changes (Jezkova and Wiens, 2016). Considering the speed at which climate scenarios are currently changing around the world, this could be a disadvantage for those groups with PNC. An essential and vital part of generating effective and climate change-sensitive conservation strategies is being able to anticipate these evolutionary changes. Considering the areas with high species diversity and ploidy levels of *Lessingianthus* found in this study, the need to conserve those areas of high climatic suitability for the species of the genus is evident. In addition, accelerated climate change and the high degree of niche conservatism between diploids and polyploids reinforce the need to conserve these areas of high diversity and/or anticipate the potential risk that these species may face.

5. Conclusions

This study shows once again that the genus *Lessingianthus* is a very complex group from a cytogenetic point of view. Our results complement currently available data and underline the importance of polyploidy in the evolution of this genus.

Our findings indicate that the diploid and polyploid populations of *Lessingianthus* can occupy the same geographical areas and have wide distribution ranges. Our analysis of the cytogeographic distribution revealed two areas with both high cytotype and species diversity: in the department of Amambay (central-eastern Paraguay) and on the border between Corrientes and Misiones (Argentina), regions that are also transition zones between biogeographic regions. In these areas, the currently protected areas are insufficient, so the design of possible conservation strategies (e.g., implementation of protected areas, sustainable management and restoration) is highly necessary to ensure their long-term persistence. Regarding the ENMs, our findings reveals that the diploid and polyploid niches overlap, and the polyploids fall almost completely within the diploid niche, indicating that polyploidization in *Lessingianthus* has not caused expansion to novel environmental conditions. PNC may explain the lack of niche differentiation between the diploids and the polyploids.

CRediT authorship contribution statement

MBA, JEF and GVdP planned the study; MBA carried out chromosome counts; GVdP conducted the maps of geographic distribution of cytotypes and ecological niche modeling analysis, MBA and JEF performed the statistical analyses; and all authors wrote the manuscript and approved the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2023.125719.

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