



# Reassessing the taxonomy of the *Libidibia ferrea* complex, the iconic Brazilian tree “pau-ferro” using morphometrics and ecological niche modeling

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## Abstract

*Libidibia* is a small genus of caesalpinoid legumes with seven species spanning from Mexico and the Caribbean to southern South America. Within this genus, *Libidibia ferrea* stands out as an iconic Brazilian tree currently classified into the varieties *ferrea*, *glabrescens*, *leiostachya*, and *parvifolia*. They comprise a species complex together with three other varieties currently accepted as synonyms (var. *cearensis*, var. *megaphylla* and var. *petiolulata*). Together they exhibit complex morphological variation, along with confusion regarding their common names and geographic distribution. Five distinct morphotypes were recognized which were compared using a morphometric study of 26 quantitative leaf characters. We also performed ecological niche modeling for those morphotypes spanning from Quaternary to the present. Principal Component Analysis (PCA) and Discriminant Analysis (DA) revealed four main clusters which also present distinct niche preferences throughout the Quaternary and current distinct geographical distributions. Based on our findings, we propose recognizing four morphotypes as separate species: *L. ferrea*, *L. juca*, *L. leiostachya*, and *L. parvifolia*. *Libidibia ferrea* and *L. juca* are small trees and shrubs, distributed respectively in the southern portion of the ‘Caatinga’ and from the Amazon to the northern ‘Caatinga’ region. On the other hand, *L. leiostachya* and *L. parvifolia* are both tall trees, predominantly inhabiting the wetter regions of the ‘Caatinga’ (*L. parvifolia*) and extending into the coastal rainforests of southeastern Brazil (*L. leiostachya*). Three new combinations are proposed and an identification key, diagnostic descriptions, and taxonomic notes are presented.

**Keywords** Caesalpineae · *Caesalpinia* · Jucá · Leguminosae · Species complex

## 1 Introduction

*Libidibia* (DC.) Schtdl. is a neotropical genus in the subfamily Caesalpinioideae (Leguminosae), consisting of seven species distributed from Mexico and the Caribbean to Paraguay and northern Argentina (Lewis 2005; Gagnon et al. 2016). It occurs mainly in seasonally dry tropical forests and woodlands and secondarily in wet forests (Ford 1995; Gagnon et al. 2016; Oliveira and Fernando 2023). *Libidibia* species are typically small to large trees with smooth or fissured bark,

bipinnate leaves with opposite pinnae and leaflets or, less frequently, the leaves singly pinnate, pentamerous and zygomorphic flowers, boat-shaped abaxial sepals, a differentiated adaxial petal (standard), ten stamens, and indehiscent, woody or coriaceous, fruits (Ford 1995; Gagnon et al. 2016).

*Libidibia* species were classified in the genus *Caesalpinia* L. for most of their taxonomic history (Tulasne 1844; Bentham 1870; Polhill and Vidal 1981; Lewis and Schrire 1995; Ulibarri 1996; Lewis 1998). The genus was reestablished by Lewis (2005) based on phylogenetic studies that demonstrated that *Libidibia* is monophyletic and not closely related to *Caesalpinia* sensu stricto (Lewis and Schrire 1995; Bruneau et al. 2008; Nores et al. 2012; Gagnon et al. 2013, 2016). More recently, a phylogenetic study with a broad taxonomic sampling in *Caesalpinia* and related genera confirmed the monophyly of *Libidibia* (Gagnon et al. 2016). Additionally, this study indicated that the Caribbean genus *Stahlia* Bello is sister to *Libidibia*, and these authors transferred the only species of *Stahlia* to *Libidibia* based on

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similarities in leaflet glands and flower morphology (Gagnon et al. 2016).

*Libidibia* species are often of great importance to local communities throughout their geographic range. For instance, *Libidibia coriaria* (Jacq.) Schldl. is the national tree of Curaçao and is locally known as ‘divi-divi’ or ‘Watapana tree’ (Sullivan 2006). *Libidibia ferrea* (Mart. ex Tul.) L.P. Queiroz is an iconic species endemic to the Brazilian flora, distributed in all regions of the country and occurring in ‘Caatinga’, ‘Cerrado’ and ‘Mata Atlântica’ phytogeographic domains (Oliveira and Fernando 2023). It is highly valued by indigenous and traditional communities, as well as urban populations (Bentham 1870; Lorenzi 1992; Carvalho 2003). Its timber is used to build bridges, and is also used to make tool handles, doors, and furniture (Gasson et al. 2009). Additionally, it is widely cultivated as an ornamental tree in Brazil and across the tropics including in Africa, Asia and Oceania (POWO 2023). In the field of medicine and pharmacology, the species is notable for its antibacterial and anti-inflammatory activities, as well as its use in the treatment of parasitic diseases such as leishmaniasis. Traditional communities often use the species in folk medicine and religious rituals (Carvalho et al. 1996; Pereira et al. 2011; Jensen 2020).

The species was initially described as *Caesalpinia ferrea* Mart. ex Tul. by Tulasne (1844). Since its first description, its complex morphological variation was recognised as three separate varieties: *C. ferrea* var. *ferrea*, *C. ferrea* var. *petiolulata* Tul., and *C. ferrea* var. *megaphylla* Tul. Later, Bentham (1870) described three more varieties: *C. ferrea* var. *glabrescens* Benth., *C. ferrea* var. *leiostachya* Benth., and *C. ferrea* var. *parvifolia* Benth. Huber (1901) published an additional variety, *C. ferrea* var. *cearensis* Huber. *Caesalpinia ferrea* var. *leiostachya* was elevated to species rank by Ducke (1953), as *C. leiostachya* (Benth.) Ducke. More recently, *C. ferrea* was transferred to *Libidibia*, and four varieties were accepted (Queiroz 2009, 2010): *L. ferrea* (Mart. ex Tul.) L.P. Queiroz var. *ferrea*, *L. ferrea* var. *glabrescens* (Benth.) L.P. Queiroz, *L. ferrea* var. *leiostachya* (Benth.) L.P. Queiroz, and *L. ferrea* var. *parvifolia* (Benth.) L.P. Queiroz. *Caesalpinia ferrea* var. *petiolulata*, *C. ferrea* var. *megaphylla* and *C. ferrea* var. *cearensis* were considered synonyms of *L. ferrea* var. *ferrea* (Queiroz 2009; POWO 2023). The species, in its broadest circumscription, exhibits significant morphological variation, especially in foliage, but also in ecology, geography, and cytogenetics (Ford 1995; Borges et al. 2012; Albuquerque 2019), resulting in considerable difficulty in delimiting the infraspecific taxa within the species.

Because of its taxonomic complexity and its diversity of uses, the infraspecific taxonomy of *L. ferrea* has remained controversial. Lewis (1987) referred to *C. ferrea* as a species complex that requires a detailed study for a more stable

taxonomic resolution. The first preliminary revision of the genus was conducted by Ford (1995), as an unpublished undergraduate thesis. Ford (1995) also referred to *C. ferrea* as a species complex. This taxonomic complexity is reflected in the confusion between common names and formal classifications, a phenomenon observed since 1860, especially with plants referred to as ‘jucá’ and ‘pau-ferro’, the two most commonly used vernacular names for this species complex. The name ‘pau-ferro’ is typically used in southeastern Brazil, as far north as Bahia and Pernambuco, while the name ‘jucá’ is used in the Brazilian Amazon, eastwards to the states of Ceará and Rio Grande do Norte in the northern part of the Northeast region (Allemão 1859; Bentham 1870; Lorenzi 1992; Carvalho 2003). When Huber (1901) proposed *C. ferrea* var. *cearensis*, he mentioned that it was known by the common name ‘jucá’, which was subsequently used in dendrological, pharmacological, and anthropological studies (Rocha 1919; Guenther 1931; Figueiredo and Silva 1967).

Some studies explicitly differentiated between ‘pau-ferro’ and ‘jucá’, suggesting that the former are always large trees, while the latter are small trees or robust shrubs, reaching two meters in height (Almeida 1943). Ducke (1953), commented that what Tulasne (1844) referred to as ‘pau-ferro’ was actually ‘jucá’, which was distinct from the true ‘pau-ferro’ corresponding to the taller trees in Rio de Janeiro and the mountains of northeastern Brazil. These confusions have a significant impact on communication regarding the biological aspects and uses of the *L. ferrea* complex, leading to inconsistencies in its recorded geographical distribution, problems with accurate identification, and difficulty in correlating species taxonomy with local knowledge and uses. Furthermore, some published studies, especially in the fields of phytochemistry and pharmacological use, have introduced new nomenclatural problems, e.g., *C. ferrea* var. *cearensis* published without the designation of a nomenclatural type (Rosenegger et al. 2017; Brito and Pontes 2021), and even the use of unpublished names, such as ‘Libidibiaceae’ (Dantas 2023). Another significant issue is that, despite the scientific community recognizing that *L. ferrea* comprises a number of varieties, these are rarely mentioned in popular articles, pharmacology, ethnobotany and phytochemistry articles, gardening and urban landscaping books and websites, in which only the species *L. ferrea* is mentioned.

*Libidibia ferrea* likely diverged from its sister species between 2.27 Ma (Gagnon et al. 2019) and 7.8 Ma (L.G.R. Souza, Federal University of Pernambuco, pers. comm.). Studies on floral biology and cytogenetics have demonstrated the presence of different cytotypes among specimens identified as *L. ferrea*, including diploid and tetraploid groups (Borges et al. 2012; Albuquerque 2019). Borges et al. (2012) suggested that the analyzed cytotypes could represent different species due to reproductive isolation resulting in morphological differences in the length and width of the flowers. On the

other hand, Albuquerque (2019) considered that there is no correlation between ploidy level, morphology, and ecological niche, concluding that the varieties of *L. ferrea* cannot be reliably separated into species based on integrative studies using molecular data and genome size, as well as niche modeling and anatomy, even though the analyzed cytotypes occur in separate environments with only small areas of geographic overlap. Unfortunately, these two studies do not mention vouchers for the analyzed specimens, making it impossible to establish correlations between the observed cytotypes with the morphology or taxa associated with the *L. ferrea* complex.

Morphometrics has been widely used for quantitatively expressing morphological differences, allowing the understanding of patterns that were previously imperceptible or overlooked, but contain valuable information in determining the taxonomic identity of a species (Henderson 2006; Costa 2009; Pedersen 2010; Pinzon 2011, Scriveranti 2013; Porter-Utley 2014; Vasquez 2022). It has been a useful tool for distinguishing taxa in different plant families, and within Leguminosae numerous studies have addressed species complexes by combining morphometrics with other tools, in most cases improving species delimitation (Conceição et al. 2007; Estrella et al. 2009; Soladoye et al. 2010; Souza et al. 2014; Morales et al. 2014; Egan 2015; Escobar 2018).

In addition to tools that use morphology for species delimitation, ecological niche modeling has been used in taxonomic studies, of both plants and animals (Raxworthy et al. 2007; Hawlitshek et al. 2011; Aguirre-Gutiérrez et al. 2014; Shrestha and Zhang 2014; Gama et al. 2017). Defining the potential niches of species can be a way to demonstrate geographical isolation between allopatric populations, thus having practical importance in species delimitation (Wiens and Graham 2005). This was demonstrated by Castro-Bonilla et al. (2022), who combined morphometric information and niche modeling and concluded that the previously accepted varieties of *Inga subnuda* Salzm. ex Benth. correspond to distinct species.

Despite the published studies on *L. ferrea* and its varieties, along with the wealth of scientific and popular knowledge accumulated on the taxonomy, uses, and cultivation of this species, there is still a considerable challenge in defining its taxonomic identity and currently recognized infraspecific taxa. There are significant differences in morphology, geographical distribution, ecology, and genetics that have been previously overlooked, both among the currently recognised varieties and among synonymized taxa. This suggests the hypothesis that different species may be recognized within the *L. ferrea* complex. In the present study we analyzed morphological variation and potential environmental niches of the taxa associated with the *L. ferrea* complex, in order to test this hypothesis and produce a stable taxonomic resolution for these iconic plants of Brazil.

## 2 Material and methods

**Material and bibliography** – This study was primarily based on herbarium specimens from the following herbaria: ALCB, ASE, CVRD, EAC, HS, HUEFS, HVASF, IAN, INPA, IPA, K, M, MAC, MBM, MO, NY, P, PEUFR, R, RB, SP, SPF, VIES, UB, UFP, US (acronyms according to Thiers 2023).

A comprehensive literature review was conducted, consulting the protologues of all taxa related to *L. ferrea* and its synonyms. Type specimens, or images of type material were studied. General morphological terminology mainly follows Stearn (1966) and Gunn (1991) and terminology used in specific treatments of the group, such as Lewis (1987), Ducke (1953), Ford (1995), Queiroz (2009), and Gagnon et al. (2016). Common names, phenological data, and geographical coordinates were mainly taken from herbarium specimen labels.

**Morphometrics** – We selected 79 specimens with evidence that they were collected in natural habitats (i.e., not cultivated) and present complete and fully developed vegetative parts. From this total, five morphotypes were chosen based on an analysis of overall morphological variation, including of type specimens. The morphotypes were named after one of the taxa currently associated with the *L. ferrea* complex: (1) ‘ferrea’ (21 specimens), corresponding to *L. ferrea* var. *ferrea*, including the type material, *Gardner 1277* and the type of var. *petiolulata* from Bahia, *Blanchet 3264*; 2) ‘juca’ (24), corresponding to *C. ferrea* var. *megaphylla*, *C. ferrea* var. *petiolulata* from Piauí according to the species protologue (although more likely from Ceará, given that the locality was given as ‘Villa do Crato’) and *C. ferrea* var. *cearensis*, as well as the binomial *C. juca*, including their respective types: *Gardner 1834*, *Gardner 2147*, *Glaziou 10646*; (3) ‘glabrescens’ (10), corresponding to *L. ferrea* var. *glabrescens*; (4) ‘leiostachya’ (9), *L. ferrea* var. *leiostachya*; and (5) ‘parvifolia’ (15), *L. ferrea* var. *parvifolia*. Where the ‘leiostachya’ and ‘glabrescens’ morphotypes are treated together, we have called them the ‘intermedia’ morphotype. The remaining type specimens were not included in the analysis as they were inadequate for the purpose of taking measurements.

The measurements were taken from mature and fully developed leaves, from the third to the fourth node from the apex of the branch. Each specimen was considered an individual in the analysis. Only leaf characters were used because most herbarium specimens have leaves, but not all specimens have flowers and/or fruits. Additionally, we observed that floral morphology is highly conserved, with little variation among the morphotypes. Physical specimens were measured using a graduated ruler with a precision of

1 mm. Photographs of the specimens available online were measured using ImageJ Software (Schneider et al. 2012), calibrated by the rulers in the herbarium images and corrected with the program. One or two fully developed leaves were measured per specimen.

A total of 26 quantitative characters were selected (Table 1). Principal Component Analysis (PCA) was conducted to assess the morphological variation among the morphotypes (Pearson 1901; Abdi and Williams 2010), and Discriminant Analysis (DA) was performed to evaluate multivariate distinction between predefined groups and determine which quantitative variables proved to be most effective for identifying these morphotypes (Fisher 1936). The statistical support for the groups recovered in the PCA was assessed using Analysis of Similarity (ANOSIM, Clarke 1993) and Non-Parametric Multivariate Analysis of Variance (NPMANOVA, Anderson 2001). All multivariate analyses were conducted using PAST 2.17 software (Paleontological Statistics Software Package for Education and Data Analysis; Hammer et al. 2023).

An identification key was created for the species recognized in this study based on the results of morphometric

analyses, incorporating all variations in quantitative measurements from the morphological data matrix, along with the inclusion of important qualitative characters for taxon differentiation.

**Niche modeling** – A total of 158 specimens of the five morphotypes were selected based on the evidence that they were native plants and not cultivated: ‘ferrea’ (30 points), ‘juca’ (66), ‘glabrescens’ (19), ‘leiostachya’ (11), and ‘parvifolia’ (32). The geographic coordinates were extracted from those presented on herbarium specimen labels or approximated based on the described locality. Niche models were calculated for each morphotype separately. An analysis was also conducted by combining the morphotypes ‘leiostachya’ and ‘glabrescens’ into morphotype ‘intermedia’, as these were not clearly separated in the morphometric analyses.

Nineteen bioclimatic variables were obtained from the WorldClim database (Hijmans et al. 2005), in raster layer files from the BIOCLIM package (BIOCLIM 2024), with a resolution of 30 arc-seconds (Table 2). This selection of bioclimatic variables allows for simulations with global climate models in different periods, covering the last interglacial

**Table 1** List of leaf characters analyzed in the *Libidibia ferrea* complex and their contributions to the first two axes of the discriminant analysis

Variable	Unit	Axis 1	Axis 2
Pinnae (A)	Number	0.2534	−0.11315
Leaflets of basal pinna (B)	Number	0.73643	−0.61943
Leaflets of median pinna (C)	Number	1.1615	−0.74362
Leaflets of distal pinna (D)	Number	0.96805	−0.86933
Leaflets of terminal pinna (E)	Number	0.96697	−0.81035
Petiolute of basal pinna (F)	mm	−0.4447	−0.10635
Petiolute of median pinna (G)	mm	−0.36907	0.011345
Petiolute of distal pinna (H)	mm	−0.62519	−0.25316
Petiolute of terminal pinna (I)	mm	−1.1811	0.022583
Distance between the two basalmost pinnae (J)	mm	−1.5248	−0.66257
Distance between the median pinnae (K)	mm	0.59482	0.24518
Distance between the distalmost pinna (L)	mm	−0.84612	0.55503
Total length of basal leaflets (M)	mm	−1.0356	−0.28296
Total width of basal leaflets (N)	mm	−0.60715	−0.05882
Width of apex of basal leaflets (O)	mm	−0.39886	−0.01755
Width of base of basal leaflets (P)	mm	−0.38441	0.027616
Total length of median leaflets (Q)	mm	−1.2273	−0.48181
Total width of median leaflets (R)	mm	−0.5536	−0.0564
Width of apex of median leaflets (S)	mm	−0.40747	−0.03881
Width of base of median leaflets (T)	mm	−0.35579	−0.08244
Total length of terminal leaflets (U)	mm	−1.4052	−0.59144
Total width of terminal leaflets (V)	mm	−0.59213	−0.08476
Width of apex of terminal leaflets (X)	mm	−0.44923	−0.04548
Width of base of terminal leaflets (W)	mm	−0.31037	−0.0419
Median distance between leaflets (Y)	mm	−0.27776	0.13542
Petiolute of leaflet (Z)	mm	−0.09857	0.001395

The letters in parentheses correspond to the vectors in Fig. 1

**Table 2** List of bioclimatic variables used in ecological niche modeling and their respective codes, based on BIOCLIM (2024)

Bioclimatic variables	BIOCLIM code
Annual mean temperature	BIO 1
Mean diurnal range	BIO 2
Isothermality	BIO 3
Temperature seasonality	BIO 4
Max temperature of warmest month	BIO 5
Min temperature of coldest month	BIO 6
Temperature annual range	BIO 7
Mean temperature of wettest quarter	BIO 8
Mean temperature of driest quarter	BIO 9
Mean temperature of warmest quarter	BIO 10
Mean temperature of coldest quarter	BIO 11
Annual precipitation	BIO 12
Precipitation of wettest month	BIO 13
Precipitation of driest month	BIO 14
Precipitation seasonality of driest quarter	BIO 15
Precipitation of wettest quarter	BIO 16
Precipitation of driest quarter	BIO 17
Precipitation of warmest quarter	BIO 18
Precipitation of coldest quarter	BIO 19

(LIG) (~ 120,000–140,000 years ago), the last glacial maximum (LGM) (~ 22,000 years ago), the mid-Holocene (MH) (~ 6000 years ago), and the present (PRE).

A clipping procedure was performed using the *r* tool (R Core Team 2023) with a script created specifically for this step. The biometric variables were applied to the entire world map, and a subset was created for Brazil to highlight the native distribution area of the morphotypes (supplementary material). An initial analysis was conducted to build the model with all 19 bio-variables in MaxEnt v.3.2.1 (Phillips and Dudík 2008), using Jackknife to measure variable importance and then selecting the ones that contributed most for a second modeling. Some default MaxEnt values were retained, with the maximum number of iterations set to 500 and a convergence threshold of  $10^{-5}$ , while modifying the random test percentage parameter to 20 (20% test data and 80% training data; Phillips et al. 2006; Phillips and Dudík 2008). The AUC (Area Under the Curve) measure was used to avoid random predictions, with a threshold set above 0.5 (Phillips et al. 2006). To display and edit the prediction model generated in ‘ascii’ format by MaxEnt, the *r* tool was used with a script for this step. The distribution maps were created using the SimpleMappr website (Shorthouse 2010).

**Species concept** – The Unified Species Concept (Queiroz 2007) was adopted in this study. The criteria for species recognition included morphological differentiation (quantitative evidence from morphometric analysis and a unique

combination of characters), habitat preference (evidence based on niche modeling analysis results), and evidence of some level of geographical isolation over the Quaternary period (results from niche modeling over the Quaternary).

### 3 Results

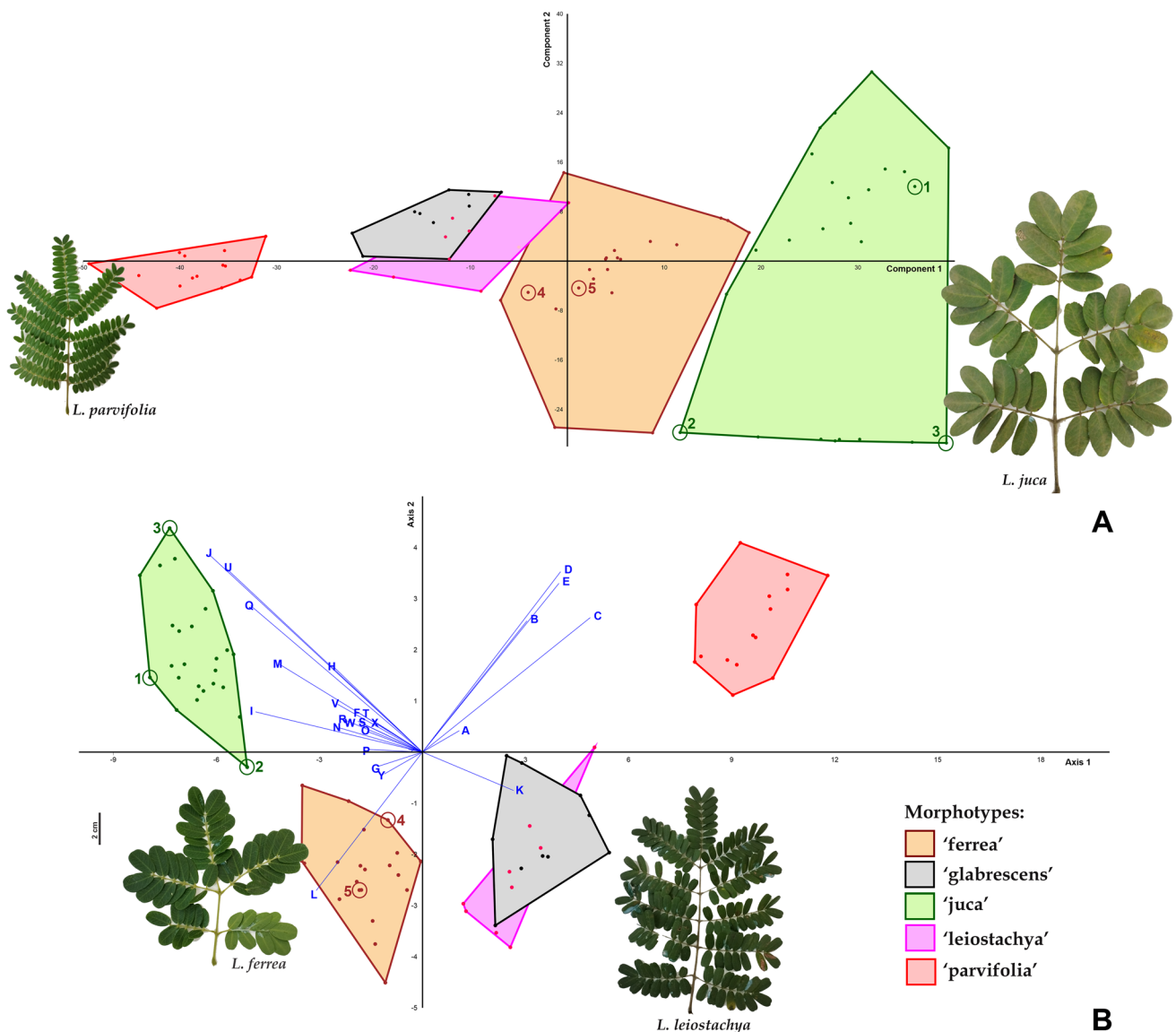
**Morphometric analysis** – The Principal Component Analysis (PCA) revealed four main clusters. The first cluster consists of representatives of the ‘parvifolia’ morphotype. The second large cluster is a combination of the ‘glabrescens’ and ‘leiostachya’ morphotypes. A representative of ‘leiostachya’ partially overlaps with the ‘ferrea’ cluster. The two following clusters are closely related but form distinct groups, ‘ferrea’ and ‘juca’ (Fig. 1a).

The first axis of the PCA accumulated 63.14% of the variation, and the first two axes together represented 80% of the observed variation. The number of leaflets in the basal pinna, followed by the number of leaflets in the distal pinna and the number of leaflets in the terminal pinna, were the characters that showed the most variation on axis 1. These characteristics distinguish ‘parvifolia’ from the ‘leiostachya’-‘glabrescens’ group. The distance between the basal-most pinnae, followed by the length of the middle and terminal leaflets, were the main characters that contributed to axis 2, characterizing the group composed of ‘ferrea’ and ‘juca’.

The cumulative variation in the first two axes in the Discriminant Analysis (DA) was 95%, with most of the data variation explained in the first axis, accounting for 80% of the variation, and the second axis contributing 15% of the variation (Fig. 1b). The morphotype groupings, with the exception of the overlap between ‘leiostachya’ and ‘glabrescens’, were similar to the results of the PCA analysis, although ‘leiostachya’ and ‘ferrea’ did not exhibit any overlap.

The most representative discriminative characters on axis 1 were the number of leaflets on the middle pinnae (C), the number of leaflets on the distal pinnae (D), and the number of leaflets on the terminal pinna (E), these determining the main diagnostic characters of the ‘parvifolia’ morphotype and separating the ‘parvifolia’ and ‘leiostachya’ groups from the others. The value of the distance between the median pinnae (K) characterizes ‘leiostachya’, which overlaps with ‘glabrescens’, as observed in the PCA (Table 1).

The values of distance between the basal-most pinnae (J), total length of terminal leaflets (U), and total length of median leaflets (Q) characterize the main diagnostic characters of the ‘juca’ morphotype. The values of terminal distance between the pinnae (L) and length of the petiole of the terminal pinna (I) determine the main diagnostic characters of the ‘ferrea’ morphotype (Table 1). The ANOSIM and NPMANOVA tests supported four morphotypes, with significant differences with a *p*-value of < 0.05. However,



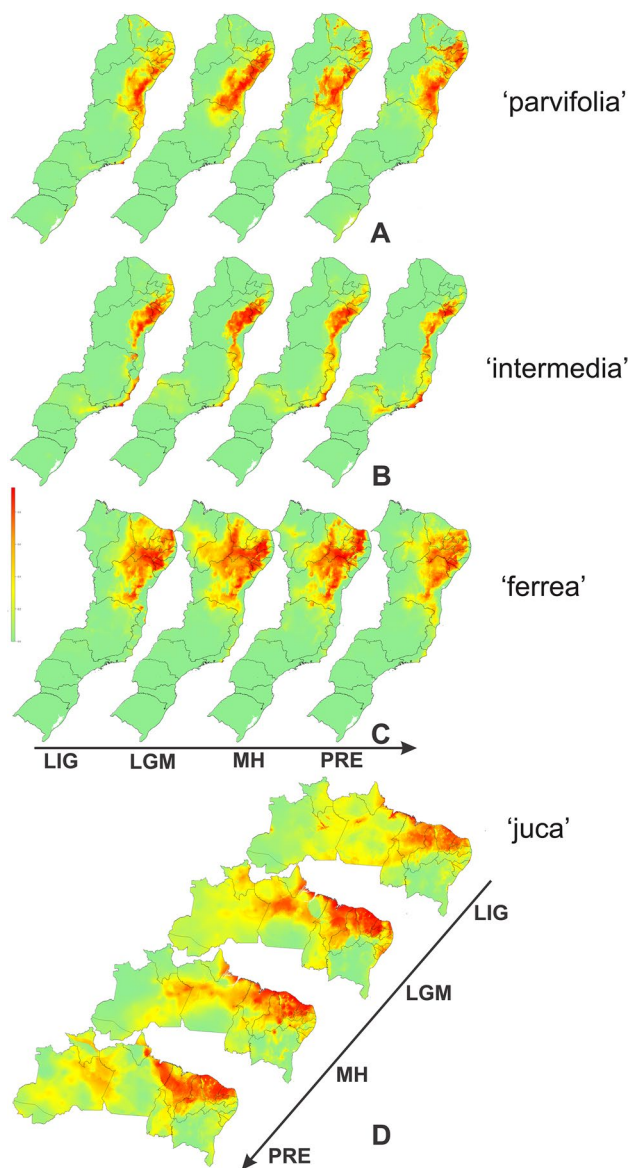
**Fig. 1** PCA (a) and DA (b) analyses of the morphotypes within the *Libidibia ferrea* complex, showing the two main axes (Axis 1 and Axis 2), based on the 26 quantitative characters. The circled points in the analyses refer to the type specimens included in the analysis, with Gardner 2147 (1) as the lectotype of *C. ferrea* var. *petiolulata*, Gardner 1834 (2) as the lectotype of *C. ferrea* var. *megaphylla*, Glaziou 10646 (3) as the lectotype of *C. juca*, Gardner 1277 (4) as the lectotype of *C. ferrea* var. *ferrea*, and Blanchet 3264 (5) as the specimen cited by Tulasne (1844) for *C. ferrea* var. *petiolulata* in Bahia. All lectotypes mentioned here were designated in the taxonomic treatment

there was a slightly smaller difference in values between the 'glabrescens' and 'leiostachya' morphotypes (Table 3).

**Ecological niche modelling** – The niche modeling results for the *L. ferrea* complex morphotypes in the analyzed periods are depicted in Fig. 2. The models show AUC values exceeding 0.9 for all morphotypes throughout the periods, signifying an excellent predictive capacity for potential distribution areas (Table 4). The selected climatic variables exhibited varying degrees of importance in shaping the individual models, both among the morphotypes and across the different analyzed periods. The 'glabrescens' and 'leiostachya'

**Table 3** Results of the NPMANOVA test, with the  $f$ -values (below the diagonal) and of the ANOSIM test with the  $r$ -values (above the diagonal)

	'ferrea'	'juca'	'leio-stachya'	'glabrescens'	'parvifolia'
'ferrea'		0.3885	0.629	0.6846	0.9855
'juca'	0.001		0.6057	0.6707	0.9898
'leio-stachya'	0.001	0.001		0.3064	0.9598
'glabrescens'	0.001	0.001	0.009		0.9852
'parvifolia'	0.001	0.001	0.001	0.001	



**Fig. 2** Ecological niche modeling for the morphotypes of the *Libidibia ferrea* complex, along the four sequentially analyzed periods: interglacial (LIG) (~120,000–140,000 years ago), the last glacial maximum (LGM) (~22,000 years ago), the mid-Holocene (MH) (~6000 years ago) and present (PRE). The morphotype ‘intermedia’ represents the combined information of morphotypes ‘leiostachya’ and ‘glabrescens’

morphotypes (referred to as ‘intermedia’ when analyzed together) were combined in our analyses due to strong overlap in the morphometric analyses. They also exhibited a more stable predictive distribution across periods when examined together, displaying a connection between both dry and humid areas (Fig. 2b).

Comparing the morphotypes in the present (PRE), ‘ferrea’ (Fig. 2C) occurs in warm and dry environments, with the most relevant variables being BIO 4 [Temperature

seasonality], BIO 17 [Precipitation of the driest quarter], BIO 14 [Precipitation of Driest Month] and BIO 16 [Precipitation of Wettest Quarter]. The ‘juca’ morphotype (Fig. 2D) is more characteristic of warm environments influenced by rainy periods, with emphasis on variables BIO 3 [Isothermality], BIO 10 [Mean temperature of the warmest quarter], BIO 17 [Precipitation of Driest Quarter], BIO 9 [Mean Temperature of Driest Quarter], BIO 11 [Mean Temperature of Coldest Quarter], BIO 19 [Precipitation of Coldest Quarter], BIO 13 [Precipitation of Wettest Month] (Table 4).

The ‘intermedia’ morphotype showed different preferences among periods, but the significant variables were BIO 14 [Precipitation of the driest month], BIO 4 [Temperature seasonality], BIO 19 [Precipitation of Coldest Quarter], BIO 12 [Annual Precipitation], BIO 17 [Precipitation of Driest Quarter] and BIO 6 [Min Temperature of Coldest Month]. The ‘parvifolia’ morphotype (Fig. 2a), like the former, exhibited variation across periods, but in the present, the most significant bioclimatic variables were BIO 3 [Isothermality], BIO 17 [Precipitation of the driest quarter], BIO 12 [Annual Precipitation], BIO 10 [Mean Temperature of Warmest Quarter] and BIO 15 [Precipitation Seasonality of Driest Quarter] (Table 4).

Regarding the distribution in the four analyzed periods, the ‘ferrea’ morphotype maintained its distribution area from the Last Interglacial (LIG) to the Mid-Holocene (MH), with a significant retreat in the present, although without pronounced fragmentation, preserving some central areas (Fig. 2c). In comparison, the distribution of ‘juca’ was characterized by more pronounced expansions and contractions compared to ‘ferrea’, extending from the central area to the north and northeast of Brazil. During the Interglacial to the Glacial Maximum period, there was a connection between the central area and a potential region within the Amazon, persisting until the Mid-Holocene but contracting in the present, maintaining the central area and small refuge fragments in the Amazon (Fig. 2d).

The morphotype ‘intermedia’ was more influenced by the drier and colder months. This morphotype maintained a central area of potential distribution similar throughout the periods along the east coast of northeastern Brazil, slightly extending inland into Bahia and reaching the southern coastline of the Southeast, with retractions in more inland areas at present. The distribution of ‘parvifolia’ varied over time, with temperature remaining the primary factor influencing its distribution, followed by precipitation values. The distribution area of this morphotype underwent significant changes in its central area across periods, but the central-eastern region from Bahia to Paraíba demonstrated higher suitability for this taxon (Fig. 2a).

**Table 4** Summary of AUC values and contribution of selected variables in previous analyses by morphotype and period, highlighting the two main variables

	'ferrea'	'juca'	'intermedia'	'parvifolia'
LIG	0.983	0.937	0.987	0.989
AUC	<b>BIO 17 (37.8%)</b>	<b>BIO 16 (59.1%)</b>	<b>BIO 17 (46%)</b>	<b>BIO 17 (67.2%)</b>
Variables (%)	<b>BIO 4 (26.9%)</b>	<b>BIO 7 (24.8%)</b>	<b>BIO 11 (26.4%)</b>	<b>BIO 1 (12.3%)</b>
	BIO 6 (13.3%)	BIO 10 (9.8%)	BIO 6 (15%)	BIO 4 (10.3%)
	BIO 11 (9.2%)	BIO 12 (6.4%)	BIO 8 (12.6%)	BIO 19 (10.2%)
	BIO 8 (7%)			
	BIO 16 (5.8%)			
LGM	0.978	0.903	0.979	0.979
	<b>BIO 4 (67.5%)</b>	<b>BIO 3 (43.6%)</b>	<b>BIO 14 (36.9%)</b>	<b>BIO 12 (30.2%)</b>
	<b>BIO 17 (18%)</b>	<b>BIO 10 (22.7%)</b>	<b>BIO 6 (22.1%)</b>	<b>BIO 10 (28.3%)</b>
	BIO 16 (14.5%)	BIO 11 (17.5%)	BIO 8 (19.5%)	BIO 14 (23.3%)
		BIO 14 (10%)	BIO 10 (13.9%)	BIO 18 (17.5%)
		BIO 16 (3.3%)	BIO 9 (7.5%)	BIO 17 (0.7%)
		BIO 19 (3%)		
MH	0.981	0.911	0.991	0.986
	<b>BIO 4 (29.9%)</b>	<b>BIO 10 (46.2%)</b>	<b>BIO 17 (24.8%)</b>	<b>BIO 4 (27.8%)</b>
	<b>BIO 10 (25.8%)</b>	<b>BIO 16 (22.8%)</b>	<b>BIO 9 (23.7%)</b>	<b>BIO 15 (25.8%)</b>
	BIO 17 (20%)	BIO 11 (20.2%)	BIO 8 (21.4%)	BIO 17 (24%)
	BIO 7 (11.6%)	BIO 8 (5.8%)	BIO 4 (14.3%)	BIO 14 (12.5%)
	BIO 11 (9.7%)	BIO 19 (5.1%)	BIO 14 (8.4%)	BIO 3 (6.2%)
	BIO 16 (3%)		BIO 10 (7.3%)	BIO 18 (3.7%)
PRE	0.986	0.915	0.991	0.985
	<b>BIO 4 (40.6%)</b>	<b>BIO 3 (27.1%)</b>	<b>BIO 14 (32%)</b>	<b>BIO 3 (30.4%)</b>
	<b>BIO 17 (27.6%)</b>	<b>BIO 10 (22.6%)</b>	<b>BIO 4 (19.4%)</b>	<b>BIO 17 (25.8%)</b>
	BIO 14 (18%)	BIO 17 (18.5%)	BIO 19 (13.6%)	BIO 12 (19.4%)
	BIO 16 (13.8%)	BIO 9 (11.3%)	BIO 12 (13.1%)	BIO 10 (12.4%)
		BIO 11 (8.8%)	BIO 17 (11.5%)	BIO 15 (12%)
		BIO 19 (6.1%)	BIO 6 (10.3%)	
		BIO 13 (5.6%)		

LIG (Last interglacial), LGM (the last glacial maximum), MH (the mid-Holocene), and PRE (the present)

## 4 Discussion

The results obtained in morphometric and ecological studies, combined with the geographic distribution of morphotypes with distinct ecological preferences and potential current and past distributions, allowed the recovery of groupings consistently differentiated by morphology, including quantitative and qualitative characters. These results support the recognition of the morphotypes 'ferrea', 'juca', 'intermedia' and 'parvifolia' as valid species, following the recognition criteria adopted within the scope of the unified species concept (*sensu* Queiroz 2007), as also adopted in the work on the *Hymenaea courbaril* complex (Souza et al. 2014). Additionally, numerous other studies on species delimitation in Leguminosae have employed morphometric analyses, either alone or in combination with other methodologies, to define the boundaries of their respective taxa, leading to their reassessment (Conceição et al. 2007; Estrella et al. 2009; Soladoye et al. 2010; Souza et al. 2014; Morales et al. 2014; Egan 2015; Escobar 2018).

Ecological niche modeling yielded satisfactory results supporting the decision to classify the five morphotypes into four distinct species, with 'intermedia' representing a combination of 'glabrescens' and 'leiostachya'. This outcome

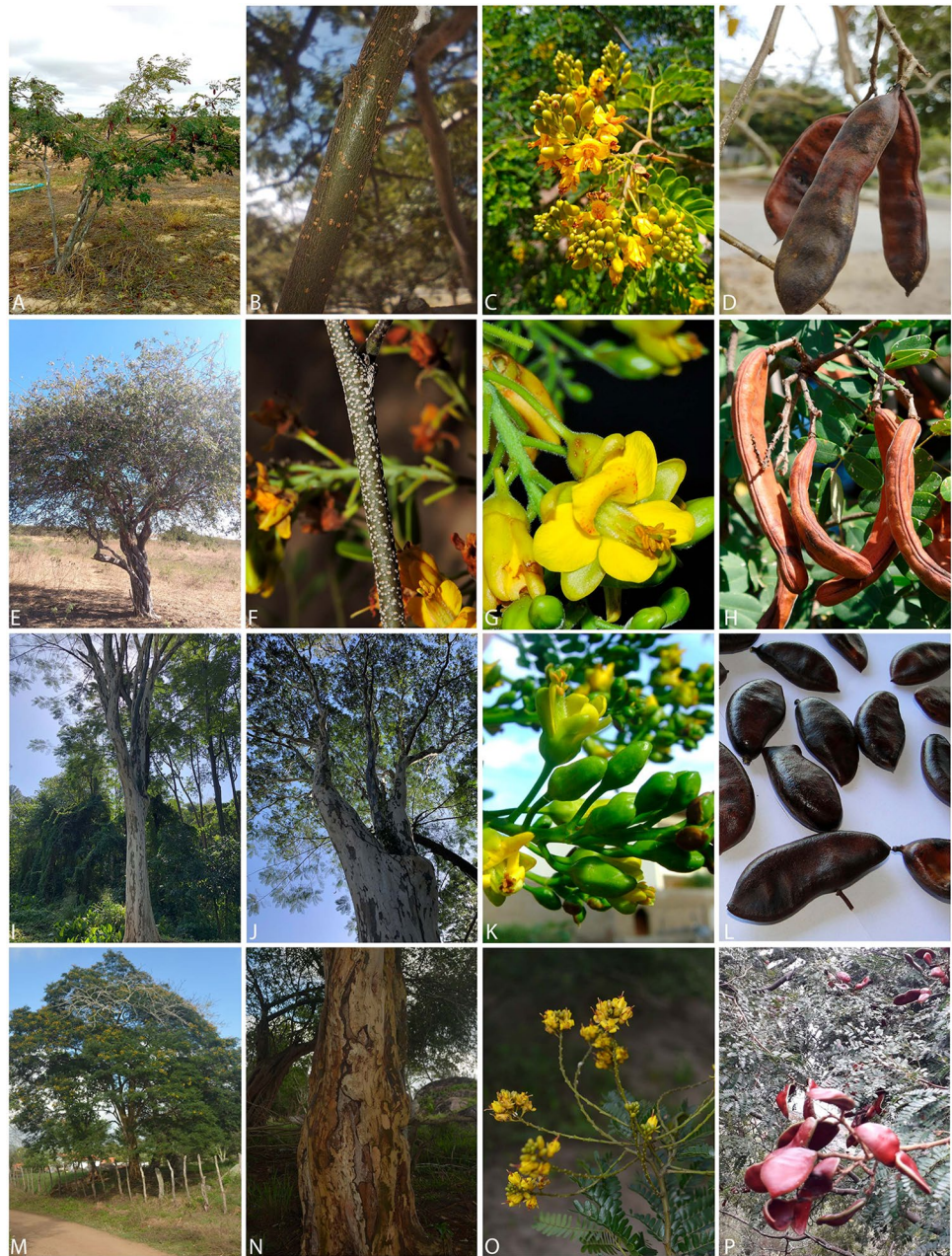
aligns with several other studies involving species delimitation using ecological niche modeling, both in plants and animals (Wiens and Graham 2005; Raxworthy et al. 2007; Hawlitshek et al. 2011; Aguirre-Gutiérrez et al. 2014; Shrestha and Zhang 2014; Gama et al. 2017).

When comparing the morphologically most similar taxa, we observed that they may exhibit both ecological similarities, linking morphotypes such as 'glabrescens' and 'leiostachya', as well as different distributions, found since the last interglacial (LIG), as in the case of 'ferrea' and 'juca'. Despite 'parvifolia' showing ecological overlap with most species, it can be present in both wet and dry areas, also displaying a distinctive morphology in its leaflets, differing from all other species. Castro-Bonilla et al. (2022) successfully delimited *Inga subnuda* by combining morphometrics with niche modeling, also employing the method of including taxa together as a single species and separated in the analyses.

Qualitative morphological characters, such as habit, lentils, indumentum on vegetative and reproductive branches, and fruit consistency, provided additional evidence supporting the differentiation of the morphotypes into four species (Fig. 3). The four major groups recovered in PCA and DA also exhibit differences in qualitative characters.



**Fig. 3** Qualitative characters of the *Libidibia ferrea* complex, showing habit, lenticels, trunk form, flowers and fruits. **a–d** *L. ferrea*; **e–h** *L. juca*; **i–l** *L. leiostachya*; **m–p** *L. parvifolia*. Photos **a** Breno Farias (<https://www.inaturalist.org/observations/90934233>); **b,d** Filipe G. Oliveira; **e** Macilio Tomaz Rocha (<https://www.inaturalist.org/observations/90934233>); **f,g** Rubens Queiroz; **h** Frederico Acáz Sonntag (<https://www.inaturalist.org/observations/90934233>); **i,j** Jéssica Moreno (<https://www.inaturalist.org/observations/123991352>), **k** Rubens Queiroz, **l** Diogo Luiz (<https://www.inaturalist.org/observations/29279842>); **m,n,o** Luciano P. Queiroz; **p** Camilla Botelho (<https://www.inaturalist.org/observations/169582145>)

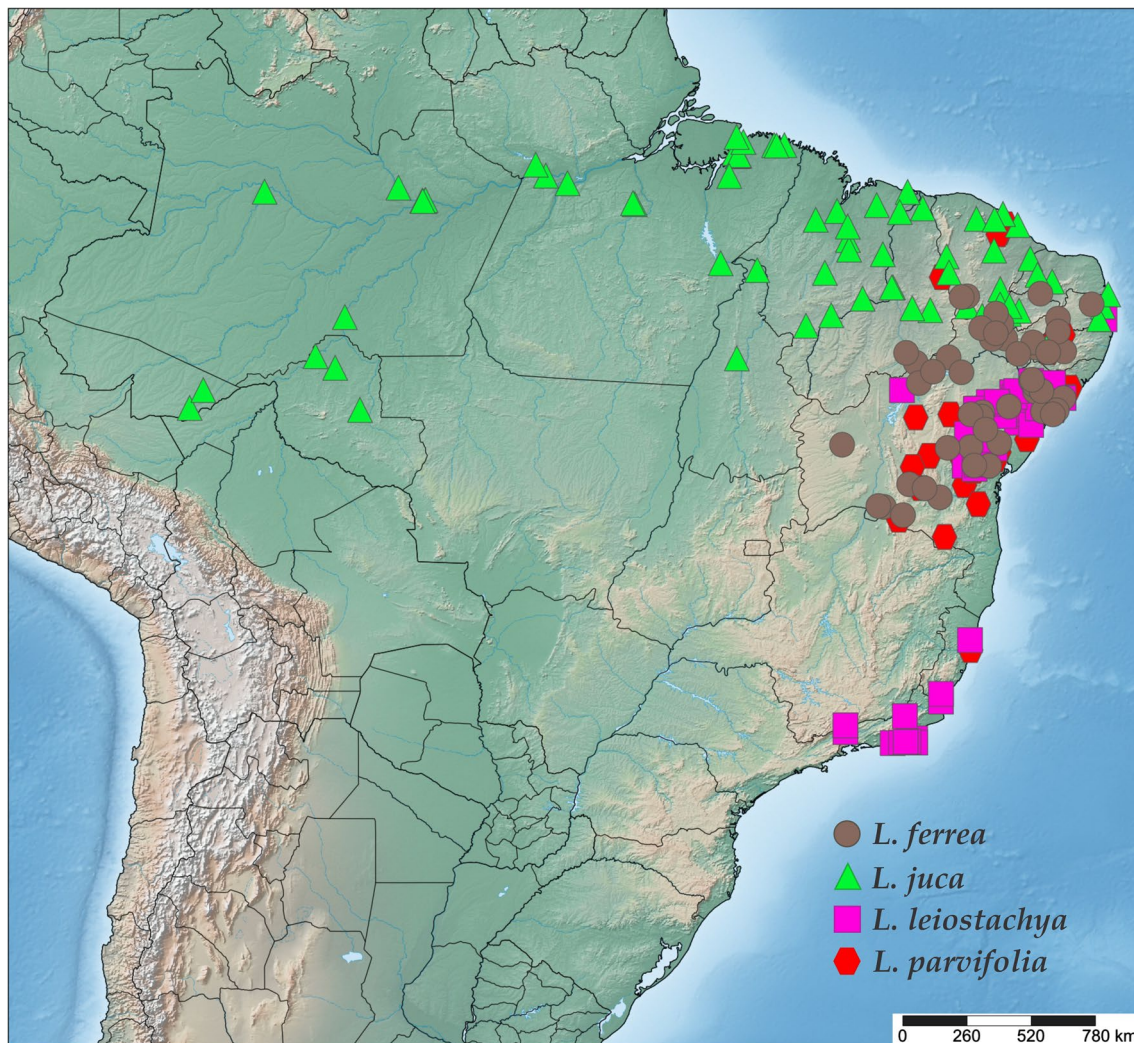


The ‘ferrea’-‘juca’ group has a small stature arboreal or shrubby habit, twisted trunks, pubescent calyx, ovary, and fruits, and fleshy fruits at maturity. In contrast, the ‘glabrescens’-‘leiostachya’-‘parvifolia’ group are large trees, with a straight trunk and branching at the apex, as well as glabrous calyx, ovary, and always glabrous and woody fruits at maturity.

The morphotype ‘ferrea’, here recognized as *L. ferrea*, formed a cluster in the morphometric analyses defined mainly by the size of the terminal leaflets, measuring 15–22 × 6–10 mm, and the distance between the two basal-most pinnae. Besides the small stature, it is diagnosed by branches with scattered lenticels, leaflets pubescent on both

surfaces, and concolorous, and fruits with a fleshy pericarp. The morphotype ‘ferrea’ has a predilection for drier areas of the ‘Caatinga’ in the interior of northeastern Brazil, from Paraíba to Bahia (Fig. 3). *Libidibia ferrea*, as delimited here, corresponds strictly to the taxon recognized as *L. ferrea* var. *ferrea* ( $\equiv$  *C. ferrea* var. *ferrea*) in various works (Lewis 1987; Ford 1995; Queiroz 2009).

In the case of the morphotype ‘juca’, here recognized as *L. juca* (Glaz.) F.G. Oliveira & L.P. Queiroz, the morphometric analyses indicated that the main diagnostic characters are the size of the leaflets, which are larger in comparison to the other morphotypes, measuring 27–36 × 10–17 mm, along with the distance between the two basal-most pinnae. Additionally, this



**Fig. 4** Distribution of *Libidibia* species in Brazil

species is a small tree with a trunk branching from the base, branches with numerous, dense whitish-yellow lenticels, and fruits with a fleshy pericarp. It occurs in the northern portion of northeastern Brazil (from Maranhão to Ceará and Rio Grande do Norte) and in the Amazon region, typically along riverbanks (Fig. 4). Both PCA and DA indicate that specimens of taxa previously considered synonymous with *L. ferrea* var. *ferrea* (Queiroz 2009) or *C. ferrea* var. *ferrea* (Bentham 1870; Ford 1995), cluster within the morphotype ‘juca’ (supplementary material), namely *C. ferrea* var. *megaphylla*, *C. ferrea* var. *petiolulata* and *C. ferrea* var. *cearensis* (POWO 2023). In addition, it includes *C. juca* (Glaziou 1906), which had not been taxonomically assessed until now.

The morphotype ‘parvifolia’, here recognized as *L. parvifolia* (Benth.) F.G. Oliveira & L.P. Queiroz, was identified in the morphometric analyses within a cluster defined by the size of the leaflets, which are smaller compared to the other morphotypes, the number of leaflets on

the distal pinnae, and the distance between the leaflets. It corresponds to the taxon previously defined as *C. ferrea* var. *parvifolia* by Bentham (1870) and accepted as a variety of *C. ferrea* or *L. ferrea* by Lewis (1987), Ford (1995), Ulibarri (1996), and Queiroz (2009). Additionally, it is a tall tree with a straight trunk and dense canopy, with many leaflets (12–15) per pinna, the leaflets glabrous and relatively small (up to ca. 9 × 3 mm), the smallest known for taxa associated with the *L. ferrea* complex (Lewis 1987, as *C. ferrea* var. *parvifolia*). It is typically a forest species, occurring in a wide range of precipitation regimes, occurring in coastal rainforests, semideciduous forests, and further inland in ‘Caatinga’ vegetation associated with mountain forests. In the northern region of Bahia to the state of Alagoas, it occurs sympatrically with *L. leiostachya* (Benth.) F.G. Oliveira & L.P. Queiroz, but the two species are clearly distinct in leaf morphology (see Notes under

these species), indicating the possibility of some degree of genetic isolation between them (Fig. 4).

The morphotype 'intermedia', which corresponds to the combination of the 'leiostachya' and 'glabrescens' morphotypes that were not separated in the PCA and DA, is recognized here as *L. leiostachya*. The morphotype 'intermedia' is defined by the number of leaflets on the distal pinnae (7–10 pairs), which are intermediate compared to the other morphotypes, by the size of the terminal leaflets, up to ca. 20 × 10 mm, and by the distance between the leaflets, ranging from 5 to 10 mm. Its habit is similar to that of *L. parvifolia*, but the leaves have larger and fewer leaflets, and the number of pinnae is usually lower. Additionally, the branches of the inflorescence are sparsely pubescent, while *L. parvifolia* has glabrous inflorescences. Ducke (1953), when elevating *C. ferrea* var. *leiostachya* to the species *C. leiostachya*, included materials from *L. parvifolia* in the variation of this species. Rizzini (1968) drew attention to this confusion made by Ducke (1953) and indicated the distinction between these two taxa. *Libidibia leiostachya* corresponds to the taxa recognized as the varieties *glabrescens* and *leiostachya* of *C. ferrea* (Bentham 1870; Ford 1995; Ulibarri 1996) or *L. ferrea* (Queiroz 2009, 2010). It is distributed in two main areas, one along the coastal region of Rio de Janeiro and Espírito Santo, in humid forests, and the second in the Northeastern region, from Alagoas to Bahia, in semideciduous forests in the transition zone between the 'Mata Atlântica' and 'Caatinga' (the 'Agreste' zone) (Fig. 4). Despite the distribution ranges of these two species having connected during the Last Glacial Maximum and mid-Holocene, they were separated during the Last Interglacial, suggesting past geographic isolation.

## 5 Taxonomic treatment

Based on the results of morphometric analyses, potential past and current ecological niches, and geographic distribution patterns, we are recognizing four distinct species within the *L. ferrea* complex: *L. ferrea*, *L. juca*, *L. leiostachya* and *L. parvifolia*.

### Key to the identification of species in the *L. ferrea* complex

1. Small to medium-sized trees and shrubs to ca. 10 m, with branched and twisted trunks; leaves with 2–4 pairs of pinnae, distal pinnae with 5–7 pairs of leaflets; leaflets pubescent on the abaxial surface, rarely glabrous; flowers with pubescent to tomentose calyx and ovary; fruits, when ripe, pubescent, with a fleshy pericarp, oblong-linear, short and with a straight apex and an undulate surface, rarely smooth ... **2.**
- 1' Large-sized trees to ca. 20 m, with straight trunk boles; leaves with 4–6 pairs of pinnae, distal pinnae with 7–17 pairs of glabrous leaflets; flowers with glabrous calyx and ovary; fruits, when ripe, glabrous with a woody pericarp, elliptical, obovate, ovate to oblong, apex usually curved, asymmetric, and always with a smooth surface ... **3.**
2. Terminal leaflets 15–22 × 6–10 mm, usually concolorous; pinnae (2–)3 pairs, separated by 18–30 mm; vegetative branches with a few scattered lenticels; inflorescences up to 10 cm long ... ***Libidibia ferrea*.**
- 2' Terminal leaflets 27–36 × 10–17 mm, generally strongly discolored; pinnae 2–4 pairs, separated by 30–40 mm; vegetative branches with numerous dense lenticels; inflorescences up to 15 cm long ... ***Libidibia juca*.**
3. Distal pinnae with 7–10 pairs of leaflets; terminal leaflets 10–20 × 5–7 (–9.7) mm; distance between leaflets 5–10 mm; petiolules 0.3–0.9 mm ... ***Libidibia leiostachya*.**
- 3' Distal pinnae with 12–17 pairs of leaflets; terminal leaflets 4–9 × 1–3.3 mm; distance between leaflets 2–3 (–4.6) mm; leaflets sessile ... ***Libidibia parvifolia*.**

***Libidibia ferrea* (Mart. ex Tul.) L.P. Queiroz, *Legum. Caatinga* 130. 2009.**

**Basionym** *Caesalpinia ferrea* Mart. ex Tul., Arch. Mus. Hist. Nat. Paris 4: 137. 1844. Lectotype [here designated]. BRAZIL, “Province of Alagoas, Tropical Brazil, *Gardner 1277* (lectotype P02736428!; isolectotypes BM!, K!). Remaining syntype: BRAZIL, “Prov. Bahia in Catingas”, *Martius s.n.* (M0217636!).

**Diagnostic description.** **Trees** 2–5(–7) m tall, with a few scattered lenticels on the branches, the lenticels rounded, oval or irregular, yellowish or grayish. **Leaves** with (2–)3(–4) pairs of pinnae plus a distal pinna, median pinnae with 6(–7) pairs of leaflets, distal pinna with 5–7 pairs of leaflets; leaflets concolor, sparsely to densely pubescent, elliptic; terminal leaflet with asymmetric base; median leaflets of the pinnae 15–22 × 6–11 mm, distal leaflets 15–22 × 6–10 mm; distance between leaflets 5–7 mm. **Inflorescences** paniculate, slightly branched, up to 10 cm long. **Flowers** 8.8–12 mm long., with pubescent calyx, brownish to rusty trichomes; ovary densely pubescent. **Fruits** 5–9.5 × 1.8–2.5 cm, oblong-linear, short and with a straight apex; valves pubescent with a fleshy, brownish pericarp when ripe and an undulate surface, constricted between the seeds.

**Distribution and habitat.** This species is native to northeastern Brazil, found in the states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, and Sergipe. It has been introduced in Asia, specifically in regions of India, Malaysia, Pakistan, and in Oceania, notably in New Guinea (POWO 2023). Its primary occurrence in Brazil is further inland, within the

areas of the Sertaneja Depression, where the driest vegetation of the ‘Caatinga’ thrives. Consequently, this species is associated with the most xeric habitats, typically within seasonal deciduous forests, woodlands, and shrublands.

**Notes.** *Libidibia ferrea* is restricted to the taxon previously denominated as *C. ferrea* var. *ferrea* or *L. ferrea* var. *ferrea*. The name *C. ferrea* was initially mentioned by Spix and Martius (1828) without a proper description, rendering the publication invalid. Tulasne (1844) referenced two specimens, *Martius s.n.* and *Gardner 1277*, differentiating the varieties *ferrea*, *petiolulata*, and *megaphylla* primarily by the length and width of the leaflets (see discussion under *L. juca*). We selected the specimen *Gardner 1277* deposited in P as the lectotype of *L. ferrea* because it presents complete leaves and flowers and was studied by Tulasne, the species' author. It is morphologically most similar to *L. juca*, sharing the habit of a tree of low stature with a twisted trunk and branched from close to its base, pubescent leaflets, flowers with a pubescent calyx and ovary, and oblong-linear, pubescent fruits with a fleshy pericarp. The two species differ mainly in the size of their leaflets, being 15–22 × 6–10 mm in *L. ferrea* (vs. 27–36 × 10–17 mm in *L. juca*) and in having sparse lenticels (vs. dense lenticels).

The species is commonly used in traditional medicine, particularly as an anti-inflammatory, using both the fruit and trunk bark. Furthermore, it is extensively planted as an ornamental tree. Its timber is also used in the construction industry and in carpentry in general (Lorenzi 1992; Carvalho et al. 1996; Pereira et al. 2011).

***Libidibia juca* (Glaz.) F.G. Oliveira & L.P. Queiroz, comb. nov.**

**Basionym:** *Caesalpinia juca* Glaz., Bull. Soc. Bot. France 53, Mem. 3b: 158. 1906. Lectotype [here designated]: BRAZIL, “Espírito Santo, Serra de Itabapoana, September–October 187...” *Glaziou 9760* (P02736930!) [possibly from Maranhão, Guaribas, and originally collected by Jobert & Schwacke; the Glaziou specimen is likely the Jobert & Schwacke material relabeled with new locality data]; remaining syntype: BRAZIL, “Espírito Santo, Serra de Itabapoana, Septemb–Octobre”, *Glaziou 10646* (P02736931!) [possibly from northern Brazil and originally collected by Schwacke or by Jobert & Schwacke].

*Caesalpinia ferrea* var. *petiolulata* Tul., Arch. Mus. Hist. Nat. Paris 4: 138. 1844. Lectotype [here designated]: BRAZIL, Piauí (‘Piauhy’), 1839, *Gardner 2147* (lectotype K 000055082!, isolectotypes NY 00958833!, NY 00958832!, P02736427!), syn. nov.

*Caesalpinia ferrea* var. *megaphylla* Tul., Arch. Mus. Hist. Nat. Paris 4: 139. 1844. Type. BRAZIL, probably Ceará (although given as ‘Piauhy’ in the species protologue), dry woods near Villa do Crato, Jan 1839, *Gardner 1934* (lectotype P02736441!, isolectotype K000055079!), syn. nov.

*Caesalpinia ferrea* var. *cearensis* Huber, Bull. Herb. Boissier, sér. 2, 1: 304. 1901. Neotype [here designated]: BRAZIL, Ceará, RPPN Serra das Almas, Crateús, *Nascimento 1315* (neotype HUEFS0211575!), syn. nov.

**Diagnostic description.** **Trees** 4–6 m tall, branches with numerous, rounded, oval or irregular, yellowish and clustered lenticels. **Leaves** with 2–4 pairs of pinnae, often plus a terminal pinna, this when present with 5–6 pairs of leaflets; leaflets discolor, sparsely pubescent on adaxial surface, densely pubescent on abaxial surface, rarely glabrous, elliptic to obovate; median leaflets (22–)25–34 × 9–16 mm; distal leaflets 27–36 × 10–17 mm; distance between leaflets 7–12 mm. **Inflorescences** paniculate, slightly branched, up to 15 cm long. **Flowers** 10–20 mm long, with a pubescent calyx of yellowish to rust-coloured trichomes; ovary pubescent. **Fruits** 6–12 × 1.5–2.2 cm, oblong-linear with a straight apex; valves pubescent, with a fleshy, brown pericarp when ripe, and an undulate surface, constricted between the seeds.

**Distribution and habitat.** The species occurs in the Amazon, distributed from the states of Acre and Amazonas to the state of Tocantins, along riverbanks, and reaching the northern part of northeastern Brazil, including the states of Ceará, Maranhão, Paraíba, Piauí, and Rio Grande do Norte. Its distribution is primarily in humid vegetation, associated with water courses. It also occurs in dry areas, occurring in shrubby and arboreal ‘caatinga’ vegetation.

**Notes.** *Caesalpinia juca* is recombined here in *Libidibia* due to the morphological similarities of its bipinnate leaves with opposite pinnae and symmetrical leaflets. Based on its diagnostic characters, such as the distal leaflets measuring 27–36 × 10–17 mm and numerous clustered lenticels on its branches, it was observed that *C. juca* shares several diagnostic features with the specimens of *C. ferrea* var. *megaphylla*, *C. ferrea* var. *petiolulata*, and *C. ferrea* var. *cearensis*.

*Libidibia juca* is more similar to *L. ferrea*, both sharing the small tree habit with twisted trunks, the similar indumentum of the leaflets and flowers, the pubescent ovary, and the oblong-linear, pubescent fruits with a fleshy pericarp. They are primarily differentiated by the size of their leaflets, 27–36 × 10–17 mm in *L. juca* (vs. 15–22 × 6–10 mm in *L. ferrea*), numerous dense lenticels on branches (vs. sparse lenticels), and usually strongly discoloured leaflets in *L. juca*. Furthermore, *L. juca* is distributed farther north and in moister habitats than *L. ferrea* as it occurs in the Amazon and in the northern part of northeastern Brazil, while *L. ferrea* is found more inland in Bahia, Pernambuco, and Paraíba in the drier forms of the ‘caatinga’ vegetation.

This species is popularly known as ‘júcá’ in its area of occurrence and is widely cultivated in Brazil, likely due to its medicinal properties (Allemão 1859; Carvalho et al. 1996; Pereira et al. 2011; Jensen 2020), which makes its natural distribution difficult to assess.

When describing *Caesalpinia juca*, Glaziou (1906) cited two specimens supposedly collected by himself in Itabapana, state of Espírito Santo (eastern coast of Brazil). However, this species is known only from the Amazon and the northern part of the Northeast region, at least 2000 km away from the locality cited by Glaziou. The specimens attributed to Glaziou originally lacked labels, and they were often relabeled after his death as materials were incorporated into the R and P herbaria. It is also well-documented that Glaziou appropriated specimens collected by other botanists and labeled them with his own collection numbers. In the case of plants from northern Brazil and cited by Glaziou as collected in eastern Brazil, it is very likely that the collections were made by Carl August Wilhelm Schwacke (1848–1904; Wurdack 1970; Prance 1971; Stafleu and Cowan 1985). In our search for material collected by Schwacke, we found a specimen collected by Clemens Jobert in Maranhão (Jobert 1162, P02736756), very similar to the specimens self-attributed to Glaziou. Jobert conducted joint expeditions with Schwacke in northern Brazil throughout the 1870s (Stafleu and Cowan 1976; Urban 1906), where the species is commonly distributed and where Glaziou made no collections. Based on all these pieces of evidence, we believe that the material Glaziou used to describe *C. juca* originated from Jobert's specimen.

*Caesalpinia ferrea* var. *petiolulata*. was described based on two syntypes, *Blanchet 3264*, collected in Bahia, and *Gardner 2147*, collected in Piauí (Tulasne 1844). The first specimen corresponds to *L. ferrea* as recognized here, and the second to *L. juca* (Glaz.) F.G. Oliveira & L.P. Queiroz. In this study, we lectotypified *C. ferrea* var. *petiolulata* based on *Gardner 2147*, and this variety is here recognised as a synonym of *L. juca*. This variety was described as having leaflets with an obtuse apex, retuse to truncate base, and sparse indumentum, which matches the diagnostic features of *L. juca*, as confirmed by PCA and DA.

*Caesalpinia ferrea* var. *megaphylla* was characterized by leaflets with an obtuse to emarginate apex, and a sparser indumentum of longer trichomes (Tulasne 1844) but it is nested within the cluster that delimited *L. juca*. The type specimen was referred to by George Gardner as collected in Piauí (Tulasne 1844), but he indicated that the collection had been made near the village of ‘Crato’, which is located in the state of Ceará.

*Caesalpinia ferrea* var. *cearensis* was described by Huber (1901) without the designation of a type. We did not find any specimen annotated by Huber, but there are materials identified with this name by Adolpho Ducke that correspond to its original description. According to Article 40.1 of the International Code of Nomenclature for Algae, Plants, and Fungi, the requirement for the designation of a type for the valid publication of a name only applies from the year 1958

(Turland et al. 2018). Thus, we are designating a neotype to stabilize the concept of this variety.

***Libidibia leiostachya* (Benth.) F.G. Oliveira & L.P. Queiroz, comb. nov.**

**Basionym:** *Caesalpinia ferrea* var. *leiostachya* Benth., Mart., Fl. Bras. 15(2): 70. 1870. *Caesalpinia leiostachya* (Benth.) Ducke, Mem. Inst. Oswaldo Cruz 51: 458. 1953. *Libidibia ferrea* var. *leiostachya* (Benth.) L.P. Queiroz, Neodiversity: Neodiversity 5(1): 11. 2010. Lectotype [designated here]. BRAZIL “prope Rio de Janeiro juxta viam ad Jacarépaguá ducentem”, 13 Mar 1868, *Glaziou 2555* (lectotype P02736434!, isolectotypes BR5218578!, K000264580! RB38759!).

*Caesalpinia ferrea* var. *glabrescens* Benth., Mart., Fl. Brasil 15(2): 70. 1870. *Libidibia ferrea* var. *glabrescens* (Benth.) L.P. Queiroz, Leguminosas da Caatinga: 131. 2009. Holotype. BRAZIL, Sergipe-Alagoas, “banks of the Rio St. Francisco”, Feb 1838, *Gardner 1276* (holotype K000056140!), syn. nov.

**Diagnostic description.** **Trees** 10–20 m tall, with sparse or dense lenticels on the stem, these rounded, oval, linear or irregular, yellowish or greyish. **Leaves** with (3–)4–5 pairs of pinnae plus a terminal pinna, median pinnae with 7–10 pairs of leaflets, distal pinnae with 7–10 pairs of leaflets; leaflets concolor or discolor, glabrous, elliptic, chartaceous to membranaceous; terminal leaflets with asymmetrical base; median leaflets 12–17(–21)×5–9.7 mm; distal leaflets 10–19×5–7(–9.7) mm; distance between leaflets 5–10 mm. **Inflorescences** paniculate, widely branched, up to 14 cm long. **Flowers** 8–11 mm long, with glabrous calyx and ovary. **Fruits** 3.5–6×1.6–2.3 cm, elliptical, obovate, ovate to oblong, apex usually curved, asymmetric; valves glabrous with a woody pericarp, and always with a smooth surface when ripe.

**Distribution and habitat.** The species is a native of eastern Brazil in the states of Alagoas, Sergipe, Bahia, Espírito Santo and Rio de Janeiro. Additionally, it has been introduced in Paraguay and Zimbabwe in Africa. It is primarily found in humid forests in Rio de Janeiro, Espírito Santo, and Bahia. It also occurs along the São Francisco River banks, between the states of Sergipe and Alagoas, which were once covered by riparian forests but are now heavily degraded.

**Notes.** Due to morphological similarities in vegetative and reproductive characteristics, *L. ferrea* var. *glabrescens* has been synonymized under *L. leiostachya*. Individuals occurring in humid areas display greater variation in the number and size of leaflets, having fewer but larger leaflets compared to plants found along the ‘São Francisco’ river. However, morphometric analyses did not discriminate between these two populations.

When Ducke (1953) elevated *C. ferrea* var. *leiostachya* to *C. leiostachya*, he included specimens of *L. parvifolia* within the circumscription of this species, leading to many

*L. parvifolia* specimens being erroneously identified as *L. leiostachya*. These species are similar by sharing a large tree habit, numerous pinnae and leaflets, glabrous leaflets, calyx, and ovary, and woody, glabrous mature fruits. However, they can be differentiated by the number of leaflets on the distal pinnae, having 7–10 pairs in *L. leiostachya* (vs. 12–17 pairs in *L. parvifolia*), leaflet size, ranging from 10–20 × 5–7 (–9.7) mm (vs. 4–9 × 1–3.3 mm), distance between leaflet pair insertion 5–10 mm (vs. 2–3 (–4.6) mm), and the presence of petiolules on the leaflets (vs. leaflets sessile).

Several authors interpreted *C. ferrea* var. *glabrescens* as a form with glabrous leaflets of *C. ferrea* var. *ferrea* (Lewis 1987; Ford 1995) or *L. ferrea* var. *ferrea* (Queiroz 2009), choosing to down-rank the significance of the differences in habit and overall leaf morphology. Our morphometric analyses did not differentiate *C. ferrea* var. *glabrescens* from *L. leiostachya*, and they are formally synonymized here.

This species is commonly cultivated in urban tree planting throughout Brazil and has been introduced in Zimbabwe in Africa, and in Paraguay (Lorenzi 1992; Simpson and Ulibarri 2006; POWO 2023). Its wood is used in house and fence construction, including for beams and stakes, and it is excellent for mixed reforestation to rehabilitate degraded areas (Lorenzi 1992).

***Libidibia parvifolia* (Benth.) F.G. Oliveira & L.P. Queiroz, comb. et stat. nov.**

**Basionym:** *Caesalpinia ferrea* var. *parvifolia* Benth., Mart., Fl. Brasil 15(2): 70. 1870. *Libidibia ferrea* var. *parvifolia* (Benth.) L.P. Queiroz, Legum. Caatinga: 133. 2009. Holotype. BRAZIL, “in sylvis catingas de interioribus prov. Bahia”, *Martius s.n.* (M0217641!).

**Diagnostic description.** **Trees** 10–20 m tall, with few, rounded, oval or irregular, yellowish or grayish scattered lenticels on the branches. **Leaves** with 4–6 pairs of pinnae plus a terminal pinna, middle pinnae with 12–17 pairs of leaflets, distal pinnae with 12–15 pairs of leaflets; leaflets concolor, rarely discolor, glabrous, elliptic to oval, terminal leaflets with an asymmetrical base, papyraceous; middle leaflets 6–9 × 2–3.4 mm; distal leaflets 4–9 × 1–3.3 mm; distance between insertion of leaflet pairs 2–3 (–4.6) mm. **Inflorescences** paniculate, widely branched, up to 14 cm long. **Flowers** 6.6–8.7 (–11) mm long, with glabrous calyx and ovary. **Fruits** 3.5–6 × 1.6–2.3 cm, elliptical, obovate, ovate to oblong, apex usually curved, asymmetric; valves with a glabrous, woody pericarp when ripe, always with a smooth surface.

**Distribution and habitat.** This species has a native occurrence from the northeast to the southeast of Brazil, found in the states of Alagoas, Bahia, Ceará, Pernambuco, and Sergipe, as well as Minas Gerais and Espírito Santo. The species is commonly found in moister sites within the

‘Caatinga’, such as mountain forests and “caatinga arbórea” (deciduous or semi-deciduous forests), as well as in areas of humid forests in the ‘Mata Atlântica’ phytogeographic domain.

**Notes.** The species is morphologically similar to *L. leiostachya*, sharing characteristics in habit, leaves, and fruits. Both have glabrous leaflets, calyces, ovaries, and fruits and are tall trees with a straight trunk and closed canopy. Due to their morphological similarities, specimens are commonly misidentified in herbarium collections as *L. ferrea* var. *leiostachya*. The differences from *L. leiostachya* are referred to in the Notes of that species.

According to Andrade-Lima (1982), *L. parvifolia*, treated as *C. leiostachya* in his work, is typical of humid areas in elevated regions of northeastern Brazil, subjected to moist winds, mainly from the southeast, and covered by forests. This elevation contributes to air cooling, regular precipitation, and increased humidity. On the slopes, the vegetation becomes denser and taller, with trees reaching up to 25 m in height and one meter in diameter, a common characteristic of this taxon.

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**Authors’ contributions** FGO and LPQ designed the study and carried out the morphometric analyses. FSS performed niche modeling analyses. FGO, FSS and LPQ carried out fieldworks. All authors contributed to the writing of the article. All authors read and approved the final manuscript.

**Data availability** The datasets generated during and/or analysed during the current study are available in the Zenodo repository, [<https://zenodo.org/records/10580269?token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6IjEyMzJhMTMwLTk4OWYtNDA0OS04NDVILTc3OTlmMzUzNzcxYSIsImRhdGEiOiJ09LClJyYW5kb20iOiJ3ODBhODcxNjk1NmZkYTUxMGJhM2NkMGJiMmZiZTNiNyJ9.7rE7BaPrISdfpcEjZV4ghuQZOoKdjQxHBdrprMvvN5YvslkSza6O-KkbONG5UIYjZNCruU3fCofq4poLjtahg>].

## Declarations

**Conflict of interest** Luciano Paganucci de Queiroz is a Guest Editor for the Brazilian Journal of Botany and the peer-review process for this article was independently handled by another member of the journal editorial board.

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